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ECOLOGICAL ASPECTS OF EVOLUTION\*  
RELATIONS BETWEEN CLIMATE AND INTRASPECIFIC VARIATION IN PLANTS<sup>1</sup>

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THE study of interrelationships between plants and climates has attracted the interest of botanists ever since the idea of evolution has prevailed. Earlier investigations were primarily observational in character, and resulted in the development of such concepts as the plant association, plant succession, climates, life-zones and climatic life forms. These contributions aided in our understanding of plant distribution, but because the workers of this era accepted the species as the fundamental unit in ecology, they did not greatly clarify our conception of the processes which have given us the great diversity that we now find within species.

In recent years other lines of research have been developed, and these are beginning to contribute materially towards filling this gap in our knowledge. These newer studies, which are experimental rather than descriptive, are aimed directly at clarifying two sets of relationships: the first is the relation of plants to each other, and the second is their relationship to environment. It is the object of this paper to review this more recent work and to outline our present conception of these relations as they

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<sup>1</sup> Pasadena symposium by Dr. Hiesey.

pertain to the members of species having a wide distribution in many kinds of environments.

It is necessary at the beginning to have a fairly clear conception of what we mean by species. In order to escape the vagaries of subjective judgments in this matter, we define species as groups whose members are able to interbreed and produce subsequent generations of offspring as generally vigorous and fertile as the original parents. To avoid the complication arising within some species containing individuals which are mutually incompatible, we include in our definition all individuals which, though mutually intersterile, can be linked together genetically through an intermediary. This definition conforms to concepts held by experimentalists from the time of Koelreuter until the rediscovery of Mendel's laws at the beginning of the present century. Even Linnaeus entertained such a concept during his later years. Its practicality and biological value have been emphasized by modern investigations on the cytogenetics of inter- and intraspecific hybrids, as pointed out by Clausen, Keck and Hiesey (1939).

#### CLIMATIC RACES WITHIN SPECIES

The diversity in the assemblage of individuals included within one species may be extensive. In general, the greater the range of climates the species is able to occupy, the greater the variety in the assembly. Turesson (1922, 1925) was the first investigator to demonstrate this clearly. Through his comparative studies on plants brought together in a uniform garden from widely scattered localities in Europe from many kinds of habitats, he was able to prove the existence of different kinds of climatic races or ecotypes. Maritime and inland, northern and southern, low- and high-altitude strains were discovered in many species. Moreover, the climatic races of widely different species showed parallel variations in regard to both morphological and physiological properties. Among the many examples of climatic races or ecotypes described by Turesson, those of *Leontodon*

*autumnalis* may be cited as an illustration of the kinds of differences found between maritime and interior, and lowland and alpine races when these are grown together in one environment (Turesson, 1922, Fig. 13, and 1925, Fig. 24).

From a close study of the differences between ecotypes, both in the wild and in garden cultures, Turesson concluded that they are hereditary in character, and that each ecotype is a product of selection by its environment. Where two races meet, due to the juxtaposition of unlike environments, hybrids were found recombining the characters of the parent races.

Climatic races of a number of species have been studied experimentally in extensive investigations recently published by the writers (1940). The broader aspects of these studies, which include confirmation of Turesson's discovery of the existence of climatic races in wild species, have been already reviewed (Clausen, Keck and Hiesey, 1941), and a historical account summarizing studies along similar lines by other investigators has been reported by Hiesey (1940). Here we shall emphasize the properties of ecotypes as revealed by their reactions in contrasting climates, for in the intensive study of ecotypes we probably have a key to the understanding not only of the relations between plants and climates, but also of certain genetic relations between plants as well.

In the investigations cited above, clone-members of different ecotypes of perennial species were brought into gardens at three contrasting altitudes in California, one located in the mild coastal climate near sea-level at Stanford University, another half-way up the western slope of the Sierra Nevada at 4,600 feet elevation in the Transition Life Zone, and a third at timberline near the crest of the Sierras at an altitude of 10,000 feet. Along this transect climatic differences are so great that in species occurring throughout this range, from five to six different climatic races or ecotypes may be found. Starting at the shore of the Pacific and passing eastward, one may encounter a

maritime ecotype, which usually clings closely to the immediate coast, and a Coast Range ecotype, typically occupying the zone between the maritime strip and the great central valley of California. In some groups, a form occurring in the Outer Coast Ranges can be distinguished from another in the Inner Coast Ranges. After crossing the San Joaquin Valley, which generally supports a grassland flora whose species seldom invade the mountains, one often finds a third ecotype in the foot-hills of the Sierra Nevada, a fourth at middle altitudes, another at subalpine elevations and finally an alpine type at the Sierran crest. In species extending to the Great Basin region, still another ecotype may be encountered. Few species are able to occupy this entire area, but many cover segments of it requiring two or more ecotypes.

Ecotypes from the Coast Ranges sometimes thrive fairly well when transplanted to the mid-Sierran station at 4,600 feet elevation, despite the fact that the winters there are severe enough to force plants into dormancy for six months. Brought to the alpine station, however, coastal races almost invariably succumb after the first winter or two. Mid-Sierran races frequently do not survive at Timberline, and even when they do, the growing season is so short that they are often unable to produce flowers or ripen seed. They decrease in vigor, but survive fairly well at Stanford. Subalpine types are generally successful in surviving in the alpine environment, but usually they are not rapid enough in seasonal development to reach maturity. The warm winters at Stanford seem to be deleterious to alpine and subalpine races, for they come out of their winter dormancy in weakened condition and seldom thrive at this station even though they may persist for a number of years. At the mid-altitude station, on the other hand, alpine and subalpine plants may attain their maximum development, but not in the case of all species. All these observations lead to the conclusion that ecotypes in general may be grown most successfully in environments most like those in which they are native.

Another point brought out in these experiments is that ecotypes differ in their degree of tolerance to new environments. Almost without exception, any ecotype may be grown under cultivation with some success in climates which are occupied by the next ecotype of that species. There are, therefore, no sharp zonal boundaries marking the regions within which a given ecotype may be successful, but within the limits of a broad climatic belt, it may thrive distinctly better towards the center than near the fringes. This is probably of critical importance for survival under natural conditions, where success in meeting competition may depend upon relatively slight points of superiority over other plants. When a plant of one ecotype is brought to a region so unsuited to it that it barely survives even under cultivation, it must certainly give way to plants of other ecotypes.

The remarkable stability of characters of each climatic race becomes evident when one studies carefully the morphological differences between ecotypes and, during a period of years, the modifications that occur after transplanting clone-members from one climatic region to another. Details of structure and general habit of growth are essentially unaltered by transplanting. There may be, however, striking modifications in size of vegetative parts, especially of leaves and stems, and in the extent of branching of flowering stems.

When ecotypes differ from each other in qualitative characters, as is usually the case, they can be distinguished from one another in any uniform environment. Frequently, however, ecotypes also differ genetically in the size of their vegetative parts, and modifications in these characters may profoundly alter one's impression of the differences between the ecotypes when comparisons are made in different sets of environments. For example, if alpine, subalpine and mid-altitude forms are grown together in an alpine garden, the forms from lower altitudes may be so reduced in stature that they superficially resemble the genetically dwarf alpine race, while

a comparison of the same races in a garden at a lower elevation would reveal striking differences in height. Modifications such as these are quickly reversible when the environment is changed, and there is no evidence of a cumulative effect taking place over a period of years.

Thus far we have been speaking of the properties of ecotypes in a general way, because corresponding climatic races in different species react in a generally parallel manner. This fact leads us to believe that in studying the ecotypes, we are dealing with fundamental categories of plants in relation to environment. There are, however, differences in quality between what may be considered corresponding ecotypes of different species. An example is furnished by coastal races of *Sisyrinchium bellum* and *Potentilla glandulosa*. The coastal race of *Potentilla* thrives when brought to the mid-altitude station at 4,600 feet, but the one of *Sisyrinchium* barely survives one or two winters, after which it dies each time the experiment is repeated. This indicates that the range of tolerance of the coastal *Sisyrinchium* is less than that of the *Potentilla*. Both plants are alike, however, with respect to their behavior at the alpine station, for there they both usually succumb the first year.

Other peculiarities may distinguish corresponding climatic races of other species, as, for example, differences in their requirements for water or light within a given climatic zone. Hence different species may occupy different niches within the same series of climatic belts. *Dodecatheon*, for example, has evolved a series of altitudinal ecotypes in the Sierra Nevada, all of which grow only in wet bogs, while *Achillea lanulosa*, which can be found in the same localities but in drier meadows, has developed a corresponding series of climatic races fitting a different series of niches. Also, alpine races of some species have been found to thrive better in cultivation at mid-altitudes than in their native environment, yet in the wild they are not found below the higher altitudes. Com-

petition probably limits such races to localities where they have some advantage over other plants.

#### COMPOSITION OF ECOTYPES

In studying ecotypes, one inevitably raises the questions: Are climatic races clearly distinguishable entities, or do they intergrade? Are they made up of relatively homogeneous assemblages of plants, or are they, like the species of which they are a part, composed of variations of minor order?

We do not have sufficient evidence at the present time to answer these questions adequately, but facts now available show conclusively that ecotypes are not homogeneous. Examples of genetic variation within natural populations have been cited from both Europe and western North America by Turesson (1922, 1925) and the writers (1940), but the significance of variations within ecotypes is not yet clear. The individuals within a natural population may not only be morphologically distinguishable from each other, but they may also react differently when their clone-members are taken to different climates. Evidence shows that certain individuals of a population may differ in their ability to survive in other environments, while others carry variations of no selective value.

An example of the kind of variation we may expect to find within ecotypes is furnished by a recent study on three populations of *Achillea borealis*. This species and its close relative, *Achillea lanulosa*, each contain well-defined climatic races. *Achillea lanulosa*, which has 18 pairs of chromosomes, occurs in the Sierra Nevada at elevations ranging from 2,500 feet to above timberline at 11,000 feet. Its most alpine forms are dwarf, attaining a height of only 15 to 25 centimeters, as contrasted with mid-altitude races which may become over one meter high. There are also differences in leaf and flower characters. The extreme forms of this species differ so markedly from each other that on first sight they would appear to belong to two species, but they are connected

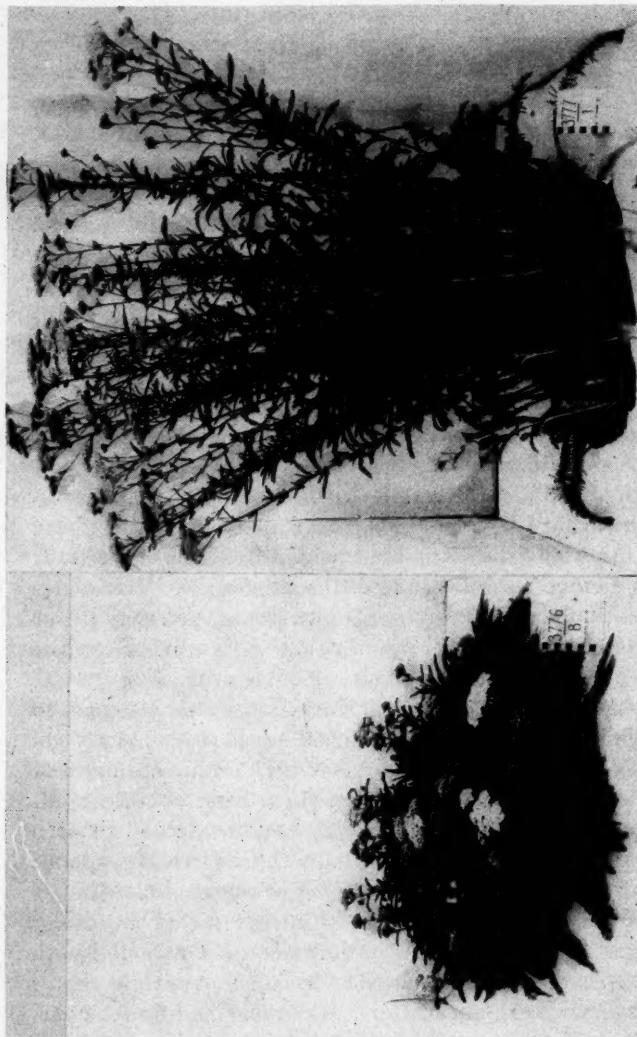


FIG. 1. Two coastal races of *Achillea borealis*. *Left*, an extreme maritime form from exposed bluffs north of Bodega Bay, Sonoma County; *right*, a taller form from a swale one mile from the sea near San Gregorio, San Mateo County, California. Both plants, growing in the Stanford garden, shown at the same scale.

by a series of intergrading forms at intervening altitudes. The other species, *Achillea borealis*, which has 27 pairs of chromosomes, has well-marked latitudinal races, and is distributed from the California coast to Alaska. The Alaskan forms of *borealis* are in some respects similar to the alpine forms of *lanulosa*, while the California Coast Range forms of *borealis* resemble very closely the tall races of *lanulosa* from middle altitudes in the Sierras.

The types of *Achillea borealis* which occur along the immediate coastal strip have the thick, heavy-textured leaves and low stems with short and compact inflorescences characteristic of maritime plants. In habitats but slightly inland, the maritime race gives way to a taller, more erect form which occurs commonly in the Coast Ranges of California. Fig. 1 illustrates some of the differences between these two races as they appear in a uniform garden. The plant on the left is from the very exposed Bodega coast north of San Francisco Bay, while the one on the right is from a population near San Gregorio, south of San Francisco, one mile from the sea. Their distinctness would suggest that they are different ecotypes, but since both occur on the maritime side of the Coast Ranges, have certain structural similarities not shared with more interior races, and are connected by intermediate forms, they might be regarded as extreme variations within one ecotype. Seed was collected from the wild populations represented by the two plants in Fig. 1, and, in addition, from a third population at Point Montara on the San Francisco Peninsula. The latter grows along an open sea-coast, but in a less exposed situation than the Bodega form.

A random sample of 60 plants of each of the three populations was grown in a uniform garden at Stanford University. All three populations were found to be variable in height, texture and size of leaves, habit of growth, vigor, earliness of first flowers and other characteristics. Since the variation in height represents quite well the degree of variation in other characters also, it is used in

Fig. 2 to illustrate the variability within each population. The herbarium specimens indicate the mean heights for each population. The frequency curves, which have been rotated 90 degrees in order to facilitate comparisons, show

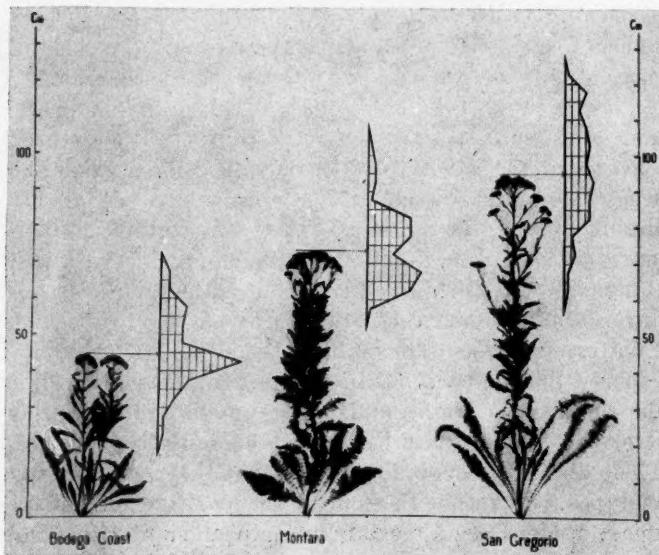


FIG. 2. Variation in height of three populations of *Achillea borealis*. Herbarium specimens show mean height of each population, and arrows point to the position of the mean values in the frequency curves. The length of the vertical bases of the curves shows the range of variation in height in each population. Class intervals are 5 cm, as shown by the horizontal lines; the distance between vertical lines represents a frequency of 2 individuals, each population consisting of 60 plants.

the variation in height within each population. The vertical base lines indicate heights in centimeters with class frequencies plotted for five-centimeter intervals. The range of variation within each population overlaps that of the others, but the mean heights are significantly different. The data may be summarized statistically as in Table 1.

The greater portion of the Bodega coast population

TABLE 1

Race	Mean height at Stanford, cm	Standard deviations of means	Differences between means, cm
Bodega coast .....	44.5 ± 1.18	9.1	28.7 ± 1.82
Point Montara .....	73.2 ± 1.38	10.6	21.8 ± 2.29
San Gregorio .....	95.0 ± 1.83	14.1	

is grouped within a relatively narrow range of variation, represented by the peak zone in the frequency curve. This suggests that the environment at Bodega may be more highly selective than the one at Montara, where the population tends to spread over a wider range of variation. The population from San Gregorio shows an even greater range of variation, as indicated by the standard deviations in the statistical summary. The San Gregorio plants grew in good soil at the west base of the Outer Coast Range in a rather protected area, too far from the sea to be within range of salt spray. Such a habitat may be expected to be less selective than the one at either Bodega or Montara.

From this analysis it appears that in each of the three habitats plants with certain ranges of variation have been selected by the environments. The three populations consist apparently of individuals whose range of physiological tolerance permits them to persist in these places.

The analysis of variation in individual populations may be carried another step. Suppose one were to select the shortest and the tallest individuals in a given wild population, and to harvest the seeds from each. A study of their progeny when grown in a uniform environment should enable one to determine whether the mother plants are sufficiently different genetically to influence the character of their offspring arising from the same kind of open pollination. Since Achilleas are self-sterile, seeds arise only by cross-pollination.

Fig. 3 depicts the results from such an experiment. Seeds were obtained in the wild from two short and two tall plants of a population at the base of Montara Mountain on the San Francisco Peninsula. The heights of the

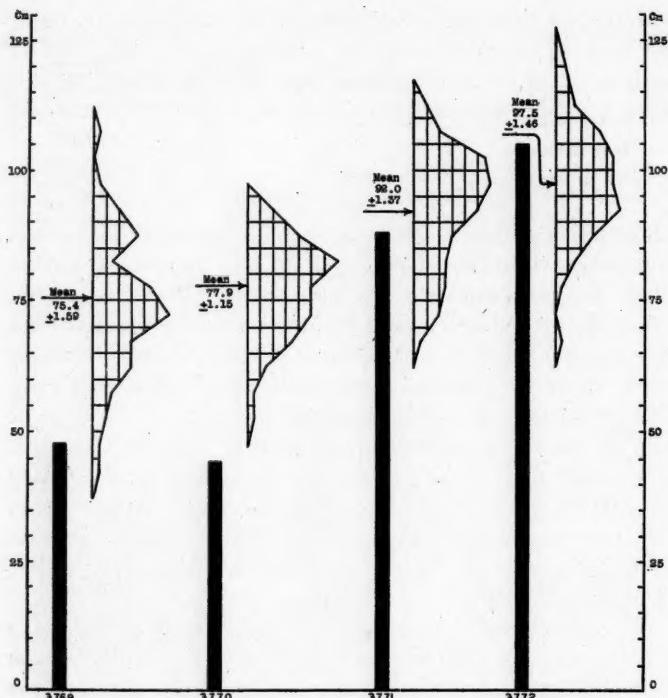


FIG. 3. Heights of four individuals from one population and of their offspring. Black columns show heights of the parent plants in their native habitat at the base of Montara Mountain, San Mateo County, California. The frequency curves, constructed as in Fig. 2, show variation in height of their offspring at Stanford.

mother plants as measured in the wild are indicated by the solid black columns, while the heights of their offspring grown at Stanford are shown by the frequency curves. It is evident that the variation in the progenies overlaps.

There is a highly significant difference between the offspring of the short parents and the tall ones, as shown in the statistical summary below. On the other hand, the differences between the two progenies of the short or the two of the tall parents are only slightly, if at all, signifi-

cant. The great differences between the short wild parent plants and the mean heights of their cultivated offspring is doubtless due in large part to modification by the environment.

TABLE 2

Culture number	Height of parents in the wild, cm	Mean heights of progeny at Stanford, cm	Difference between means, cm
<b>Short parents :</b>			
3769.....(60 offspring)	48	75.4 ± 1.59	2.5 ± 1.96
3770.....(62 " )	44	77.9 ± 1.15	<b>14.1 ± 1.79</b>
<b>Tall parents :</b>			
3771.....(62 " )	88	92.0 ± 1.37	5.5 ± 2.00
3772.....(54 " )	105	97.5 ± 1.46	

The heights of the offspring of the short parents, as shown in Table 2, do not differ significantly from those of the Point Montara population listed in Table 1. Likewise, the progeny of the tall plants do not differ significantly from those of the San Gregorio population. From this it appears that the Montara Mountain population, which came from a protected canyon no more than a half mile from the sea, consists of a mixture of truly maritime and more inland types.

If such a mixed population were divided into two parts, one of which was taken to Point Montara, and the other to the more protected situation at San Gregorio, it would be expected that within a few generations natural selection would change the composition of the two to yield populations as unlike as those now inhabiting these places.

#### SYNTHESIS OF NEW CLIMATIC RACES

Since the ecotypes of a species are interfertile, it should be possible to synthesize new races fitted to new climates by crossing and selection. As yet little work of this kind has been recorded. The writers have on hand unpublished data from a number of second and third generation populations of inter-ecotype crosses in the annual California tarweeds, of the sunflower family. In

all such populations, segregating recombinations of characters characterize the  $F_2$  and  $F_3$  cultures. An analysis of this kind is being carried a step further in the perennial species *Potentilla glandulosa*. Not only the morphological characters, but also the survival capacities of the second generation offspring are being tested in three very different environments. Preliminary studies made to date point to interesting conclusions.

*Potentilla glandulosa* occurs over a wide range of climatic extremes in the Pacific Coast region, and has produced a large number of ecotypes. The species has 7 pairs of chromosomes in all of its forms. A climatic race from the foothill region of the Sierra Nevada at 2,500 feet elevation was crossed with an alpine form from near tree-line at 10,000 feet. The foothill type is unable to survive when brought to alpine conditions, and the alpine form declines markedly in vigor when brought to near sea-level at Stanford. Both thrive at middle altitudes. The  $F_1$  hybrid was vigorous and intermediate not only in morphological characters, but also in its reactions to transplanting to different altitudes. The  $F_2$  plants are in general as vigorous as the original parents, and display a complex segregation of characters, some with evidence of linkage. The parents differ markedly in stature, habit, size of leaves and stems, pubescence, anthocyanin content, earliness of flowering, frost resistance, and in size, color and shape of petals and seeds. The uppermost herbarium specimens of Fig. 4 show some of the differences between the parents, as seen when both are grown in a garden at middle altitudes in the Sierra Nevada. In the same figure, below, are shown specimens of a few  $F_2$  plants also grown in the same garden.

Each individual of a population of 577  $F_2$  plants was divided into three clone-members, and in 1938 the triplicate sets were planted at three contrasting stations, one near sea-level at Stanford, and two in the Sierra Nevada, one at 4,600, the other at 10,000 feet. After three years' exposure to these different climates, it is now becoming

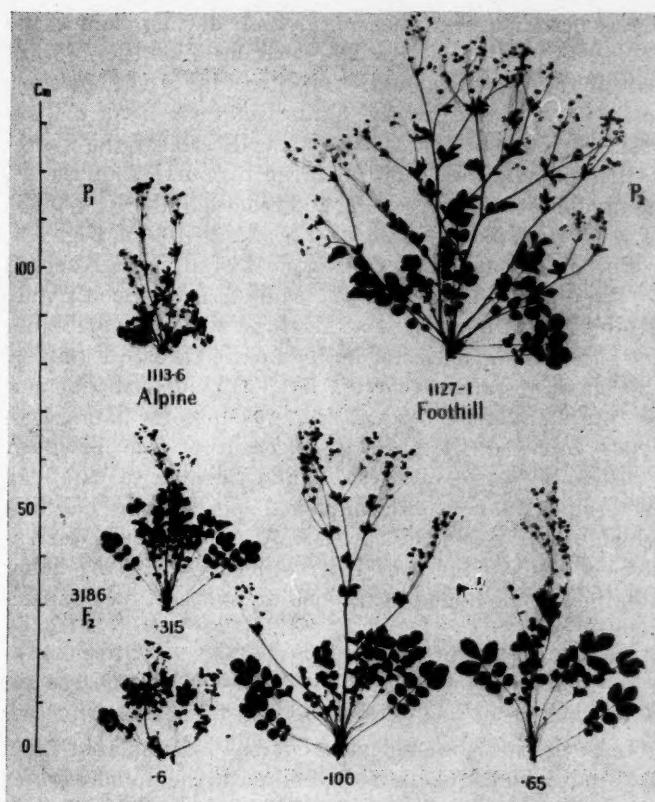


FIG. 4. Alpine and foothill ecotypes of *Potentilla glandulosa* and samples of their  $F_2$  offspring. Plant 1113-6 is from Slate Creek Valley, Mono County, California, at 10,000 feet elevation; 1127-1 is from near Oak Grove, Tulare County, at 2,500 feet. Specimens of all plants taken from the same garden at 4,600 feet elevation.

clear that certain individuals, like the plant -315 in Fig. 4, react in many ways like races native in the coastal region outside of the area of either parent. They make their most vigorous growth at Stanford, grow fairly well at the mid-altitude station, but fail to survive in the alpine garden. Other plants, like -6 of Fig. 4, are definitely

alpine both in appearance and in their development at the three stations. Also plants reacting like the foothill parent are fairly frequent. The parental types, however, have never been exactly duplicated, not a surprising result in view of the relatively small size of the segregating population. Quite a large proportion of the  $F_2$  plants more or less resemble and react like the  $F_1$  hybrids of this cross, as for example, the plant -100 of Fig. 4.

Perhaps the most interesting class of all is represented by the plant -65 shown in the same figure. Such plants exhibit exceptional vigor at all three stations, combining the survival capacities of both climatic races. Plants of this class, and those reacting like -315, suggest that new ecotypes may arise through the crossing of existing ecotypes followed by natural selection of the progeny. Presumably some of these should be able to establish themselves in new environments—possibly in habitats which may arise in the future. A number of  $F_3$  derivatives of some of the more interesting  $F_2$  plants are being obtained in the hope of establishing new ecotypes experimentally.

#### CURRENT CONCEPTION OF PLANT-CLIMATE INTERRELATIONSHIPS

In reviewing the evidence that has accumulated from the studies on the properties of climatic races, one arrives at a highly dynamic concept of the interplay between plants and their environment. We find the members of a species occurring as natural populations in places favorable for their survival. Within populations, hereditary variants occur, some of which may possess physiological qualities that give them the potential capacity to survive in different kinds of places. Other variations seem to have no significance for survival, representing random differences that are not incompatible with the main requirements of existence in their environment.

In comparing one population of a species with another from the same climatic belt in a uniform garden, we may

be able to find significant differences between them. These differences may be expressed statistically, and, like those of the individuals within a population, may or may not be of significance for survival.

As we extend our studies to populations in different climates, we notice that the differences attain a larger order of magnitude. We arrive at a point where some taxonomists begin to wonder whether they are dealing with another species or merely with a variety or subspecies. These are the climatic races, or ecotypes. Sometimes they are distinct enough morphologically to be named as subspecies. Whether or not anyone gives them a name, they are important components of the species, for they play a basic role in its struggle to occupy existing environments. If the species has been able to establish itself in a wide range of climates, we may expect to encounter a series of ecotypes, the most unlike of which may be so different morphologically that even conservative taxonomists, lacking experimental evidence, may call them different species. In some plant groups it is evident that genetic barriers have arisen between members which probably started on their careers of differentiation as ecotypes of one species. These barriers make them, by our definition, distinct species. The ecological significance of these groups may not be changed by this circumstance, but the genetic barrier prevents free interbreeding between their members.

Through studies on the reactions and survival capacity of clone-members of various races in contrasting climates, we know that each climatic race has a certain range of tolerance to changes in environment. This permits it to grow in a variety of places, in some better than in others, but never in a climate out of its range of tolerance. Transplanted members of a clone may become temporarily modified in various ways when brought to different climates, but the modifications do not erase the differences between climatic races. In most cases they even emphasize them.

When two climatic races of a species are hybridized, present evidence indicates that their second generation offspring may segregate types with many recombinations of characters and different capacities for survival in diverse environments. Thus, through crossing and selection, new ecotypes fitted to new habitats may arise.

We still have much to learn about climatic races. Little is known of their biotypic composition or of their exact interrelations to one another. Furthermore, the dynamics of their precise relations to the environment have not been explored. To illuminate these, critical studies on the comparative physiology of climatic races are necessary.

#### LITERATURE CITED

- Clausen, J., David D. Keck and William M. Hiesey  
1939. *Amer. Jour. Bot.*, 26: 103-106.  
1940. *Carnegie Inst. of Wash. Publ.* No. 520. vii + 452 pp., illustrated.  
1941. *AM. NAT.*, 75: 231-250.  
Hiesey, William M.  
1940. *Bot. Rev.*, 6: 181-203.  
Turesson, G.  
1922. *Hereditas*, 3: 211-350.  
1925. *Hereditas*, 6: 147-236.

## SOME PHYSIOLOGICAL ASPECTS OF THE PROBLEM OF ECOLOGY AND EVOLUTION

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It is not an easy task for a plant physiologist to talk on a symposium on ecology and evolution. However, there are a few aspects of evolution which can be better understood if one knows the physiological basis of them. One of such aspects is the invasion of land by plants. The problem of water uptake and root development is of particular interest in this respect.

To water and marsh plants the uptake of water presents no special problem because the water flows freely to them whenever it is needed. To true land plants, however, water uptake is more difficult, because according to the newest investigations on water in soils it appears that even at field capacity the water in the soil is practically immobile. This means that land plants growing on soils with a low water table have to grow after the water for the greater part of their life. This requires a well-branched and fast-growing root system. Grasses, for instance, have such a root system. The growth of their root system is well illustrated by the fact that a single rye plant produces over 140 million root hairs and 130,000 larger roots on a single day and that the total length of these root hairs produced on a single day amounts to over 60 miles.

The earliest known land plants, the Psilopsida, were marsh plants. They occurred at the end of the Silurian, according to some estimates 370 million years ago. They had a simple structure, had neither roots nor leaves. The lower part of the axis was a rhizome with or without absorbing hairs. These early plants are very well preserved and due to the peel technique their structure is

better known than that of many plants living to-day. The plants of the Devonian and the Carboniferous were also plants living in the mud along the margin of shallow seas. Their root system was adapted for life under these conditions. The roots of the Lepidodendrids for instance were hollow and showed a similar type of structure as is found at present only in Isoetes.

The great development of true land plants probably followed the general rise of land which occurred during the later part of the Tertiary. This great development of herbaceous plants took place during the Pliocene and the Pleistocene and coincided with the appearance of man.

## HABITAT SELECTION AMONG HIGHER VERTEBRATES AND ITS RELATION TO INTRASPECIFIC VARIATION

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IMPRESSIVE in the experience of the vertebrate taxonomist is the almost universal phenomenon of geographic variation within species. In birds and mammals, more than in any other groups of organisms, this variation has been perceived as an important forerunner of specific differentiation. We need not search through many genera before we encounter one of the *Grenzfälle* of Rensch, a borderline case between racial (subspecific) and specific differentiation. So generally convincing is the evidence to show that many species in these classes of vertebrates have arisen from geographic races that suggestions to the contrary for other groups of organisms scarcely diminish the importance that intraspecific, geographic variation holds in the mind of the vertebrate zoologist. Geographic variation indeed appears as a critical way point in speciation.

Geographic gradients in characters, the clines of Huxley, whatever their origin, are profoundly affected by barriers to distribution which serve as imperfect isolating mechanisms, short of the absolute isolation of infertility. These imperfect or impermanent isolations break up an otherwise even gradient in a character, checking the diffusion of genes along the geographic gradient system. Further, the mathematical studies of the genetics of populations of recent years (Wright, 1931; Dobzhansky, 1937; and others) have properly laid stress on the important differentiations that can take place in a system of small, partly isolated populations within species; in each of these, random fixation of genes may occur, establishing thus trial types, some one of which may flower

into prominence as a well-adapted population that may come to replace some or all of the others. Without further survey of these view-points, it should be clear that isolating devices of the lowest levels have much significance.

In classifying barriers, Grinnell (1928: 433) listed a number of types beside the obvious tangible barriers of water to land-dwelling vertebrates and land to aquatic kinds. These were: "(1) Increase or decrease in prevailing temperature beyond certain critical points . . . ; (2) increase or decrease in prevailing humidity of the air . . . ; (3) local modification in available food supply beyond that which, in sort and amount, is sufficient to support a given animal of certain specialized ability to use it; (4) the limits of a territory affording [safe] places suitable for use . . . as dens or nests for the young . . . in accordance with the breeding instincts of the species; (5) the limits of a territory providing safe places or refuges," for retreat or rest.

The last three requirements, food, dens or nests, and refuge places, absence of any one of which constitutes a barrier, may be roughly grouped as the factors of habitat, and the biotic associates figure largely in these. The question may be posed, Which of these barriers is the more generally important? This is in reality a question impossible to answer. As any ecologist well knows, at one point it may be one factor, elsewhere, another that actually limits distribution of a species. Further, it is my belief that each species is a problem in itself, and generalizations about barriers to groups of species may lead to many inaccuracies and pitfalls. Let us urge full knowledge of the factors controlling the presence of individual species, to be sure in relation to their biotic associates, before we take off in thin air and deal with communities alone.

If some measure of generalization be permitted me, it can be claimed that barriers, and hence isolation, result most often not from tangible barriers but from the less

distinct factors. This is implied in Grinnell's simple statement (1928: 430, 442): "There is no species of [terrestrial] vertebrate animal that exists everywhere in California; every species is restricted in its occurrence more or less short of the entire area of the State," that is, short of the water barriers. "Barriers to distribution which are effective in absolute degree are really in small minority." Among the intangible factors, appropriate stress has fallen in late years on the organic habitat. Most often occurrence seems to be governed by presence of plant associations suitable to the varied needs of the vertebrate species. Less often in homoiothermic animals is an absolute barrier of tolerance to temperature or humidity reached short of the limits of the plant association which the animal frequents.

By way of illustration, the chestnut-backed chickadees occur as three geographic races along the coast of California, *Penthestes rufescens rufescens* south from Washington and Oregon to Sonoma County, in the Douglas fir, redwood, Monterey pine and tan oak associations; *P. r. neglectus* occurs from Point Reyes to Sausalito in Marin County, in the same associations; *P. r. barlowi* is found from San Francisco south to Monterey County in comparable associations. The barrier between *P. r. rufescens* and *neglectus* is a gap in the forests in southern Sonoma County, that between *neglectus* and *barlowi* the water gap at the Golden Gate. It must be understood that the species does not encircle San Francisco Bay to the east. There are no water barriers of significance to these chickadees here, but there is great discontinuity of the plant associations to which they adhere. The species has come down from the Santa Cruz Mountains to San Jose at the south end of the bay in artificial plantings in the city and has extended even beyond to the east, but it has not established itself in the climatically more favorable redwood canyons of the east-bay hills back of Oakland. It seems to have been prevented from doing this solely by the discontinuity of the plant environment.

In southern Sonoma County, the red tree mouse (*Phenacomys longicaudus*), closely dependent on Douglas fir (Benson and Borell, 1931), finds its southern limits. Excellent stands of this tree occur to the southward in Marin County, but no tree mice have gotten across the intervening grasslands.

In the city of San Francisco, there are essentially no brown towhees (*Pipilo fuscus*), although artificial park land in Golden Gate Park is like that inhabited elsewhere around the bay. Contrary to the preceding instances of limitation, the factor here seems to be temperature or perhaps temperature with wind and fog. Towhees occur fairly commonly on the peninsula to the south among similar plant associations but in more protected areas.

Granting the presence of these various barriers, we now come to the problem of how they actually operate to check distribution. Most species of vertebrates are not given to wandering. Animals in general do not wander but become much attached to a "locale" and stay in "place" unless forcefully ejected. They are more like plants in this respect than we are likely to realize. Outward pressure against the barriers comes of course through population increase. Young animals do not disperse at random, accidentally; they are shouldered out and forced to pioneer. The mobility of most species of higher vertebrates permits concentration of the young in the barrier regions.

But even under this pressure at the barrier, is the pioneering attempt a trial of all kinds of new situations? Definitely this is not so. Adoption of a new, trial area involves selection according to instinctive, and perhaps also habitual, preferences of the animal. Dispersal against or through the barriers is only partly trial and error; delicate perceptions and responses are involved.

In the case of birds, there is to be seen a perfection of [the pioneering] process involving less sacrifice of individuals than in the case of rodents. A lesser rate of reproduction is required. . . . We see the operation of a more refined preference on the part of the individual—by virtue of which each

scout is able . . . to look about, move freely, and *choose* surroundings consistent with the peculiar structural needs of its species, for food, for shelter, and for safe breeding places. The [young] Song Sparrow taking part in post-breeding dissemination . . . does not blindly content itself with an attempt to find subsistence on grassy upland, or in a forest, or in dry chaparral, but keeps going, seeks out locally its own "natural" type of habitat, the stream-side thicket—the ecologic niche of its species. By the exercise of choice in the selection of habitat, a great saving of individuals is accomplished. . . ." (Grinnell, 1928:441.)

There are, then, many psychologic factors in choosing and in adhering to a particular habitat. This is the essence of the idea of habitat selection as employed by Lack (1933); the process might appropriately be called perception of adequate environment. It is an operation in birds not confined solely to young individuals but occurs also in the great number of migratory species each season at the end of each migratory flight and indeed often along the route of the migratory flight. Of course the most critical selection with respect to evolution comes on the breeding ground, since pairing usually takes place here rather than in the areas occupied in winter. Old birds often return to exactly the same nesting territory chosen in preceding seasons, apparently through memory of local detail. But this can not be true for all individuals. An old bird may find its original territory preoccupied when it arrives, or the territory may be radically altered so as no longer to be suitable. The individual must again search and choose, to be sure usually in the immediate vicinity of the former territory. The opportunity to select is therefore frequent and recurrent in such species.

In making a selection, just what does the animal perceive? It seems impossible that there is a highly intelligent evaluation of the favorable factors at a given locale, but instead an automatic, instinctive reaction, even though quite delicately adjusted, to a few key aspects of the environment. What these key characters are is of course difficult to prove; and they are not easily tested through experimentation. Intensive observation of the

reactions of animals in the wild may nonetheless narrow down the field of possible clues employed by them in habitat perception.

Lack (1933) comes to the conclusion that in many species of birds the height, and we may add spacing, of the vegetation is the prime factor in choice of habitat. His example of the tree and meadow pipits (*Anthus trivialis*, *Anthus pratensis*) is instructive. These two species, of essentially identical structure, both nest on the ground and their feeding habits would appear to be the same. The tree pipit occurred (p. 247) "regularly in open heath country identical with that frequented by the . . . Meadow Pipit provided one or more fairly tall trees were present." In a treeless area, he "found a pair of Tree Pipits breeding close to a telegraph pole. The only use to which the tree, and in the last case the pole, is put by the Tree Pipit is as a perch to which to fly down towards [at] the end of its aerial song. The Meadow Pipit has a very similar song but normally ends it on the ground." Of course we may remark that a tree pipit in a fairly well-forested area might be guided in its selection of territory by perception of some spots of open ground.

Olive-sided flycatchers (*Nuttallornis borealis*) along the Pacific coast nest in forests of tall, fairly open coniferous trees. Their nests are placed well up in the trees and their foraging and singing radius comprises the upper airways and exposed tree tops. To the surprise of many observers, this North American species has invaded the plantings of tall eucalyptus in the cool coastal belt and has established itself locally in these. The chief thing in common about the eucalyptus and the conifers is their height. The insect fauna about them, the local nest emplacements in them, and the retreats within the leafy crowns must all differ markedly. Olive-sided flycatchers in spring migration stop briefly en route in places where they do not nest. Regularly in my experience these way points in migration provide high perches of commanding view. The factor of height seems to be

the first consideration in habitat selection in this species, even though subsequently other things may be perceived which influence continued residence through the summer.

Because an animal has an instinct to select and operate in a certain habitat, is it as a species actually limited morphologically and physiologically to this environment? Is this habitat as chosen the only one that would be adequate or approach an optimum for the species? It seems that sometimes it is not, and that the selection may limit the occurrence of the species far short of limiting factors involved in nutrition, reproduction and safety from predators.

Lack takes an extreme position in emphasizing that limitation through the psychologic factor is independent of the other requirements for existence of the animal. The instinctive selection is admittedly gauged to restrict the species to an environment with which it can cope, but within the limits of tolerance only a small segment of the range in possible habitats is used. This viewpoint is apparent in Lack's analysis of the meadow pipit, which selects an area with trees so that it may sing from them, a real though purely psychologic need. More striking yet is the comparison of the reed and yellow buntings (1933: 248): These two species

of the same genus [are] both common on the Breckland, the former in marshy districts, the latter in drier districts, along the hedgerows and the edges of heaths. . . . The two show no overlap of habitat. What factor or factors caused the marked difference? The nesting sites of the two seemed similar, both being in thick vegetation on or slightly above the ground. Their breeding habits seemed similar. So far as known neither possessed structural or other adaptations to its particular habitat. The food of the two species is mainly vegetable, especially seeds, while in summer insects of many orders are taken. The sole difference is that the Reed Bunting mainly eats *marsh* plants and insects, the Yellow Bunting mainly those of drier situations. . . . Since both have such a varied diet one cannot suppose that so slight a difference, even if appreciable to the birds (which is doubtful), could cause such a marked difference in distribution. It seems clear that both species utilise the food that happens to be commonest in their respective habitats.

After citing one example of a reed bunting, which

reared a family several miles from a marsh, as an exception which proved that this bunting could be successful in the habitat of the other species, he concludes (p. 249):

There therefore seems nothing in the environment to compel the difference in distribution. The remaining possibility is a psychological factor. In the species previously considered [pipits, and others] a psychological limit could be correlated with a definite part of the bird's behaviour. In the present case there were no differences in the behaviour of the two species which could be correlated with differences in the habitats.

It is my opinion that Lack has passed rough-shod over many possible limits of tolerance in these species, limits which could be tested only through much more careful analysis and which might reveal some significant average differences in the species that in the long run would fit them better for the particular habitats they select. The exception he cites of successful breeding outside the usual habitat proves little. We would not expect the tolerances of these species to be so sharply drawn as to exclude occasional exceptions.

In spite of these criticisms, reflection upon parallel examples where there is habitat selection, as in our closely related species of chickadees, *Penthestes gambeli* and *Penthestes atricapillus*, or white-footed mice of the species *Peromyscus eremicus* and *Peromyscus crinitus*, leaves one with the opinion that habitat selection is a real limiting instinct, often holding the species in check somewhat short of other limitations. This instinct is just as much a part of the vital equipment of the species as a structural adaptation. Mind and body are after all one when we consider the success of the organism or the species as a whole. The general importance of this selection in evolution lies in the fact that it may constitute the first barrier to distribution, and a fairly rigid one, which brings about incipient isolation.

A negative way in which habitat selection functions in evolution is through unduly limiting the exploration of new areas or slightly different habitats by a species. I have been impressed with this in studying (Miller and McCabe, 1935) the geographic variation in two species of

the same genus, Lincoln sparrows (*Melospiza lincolni*) and song sparrows (*Melospiza melodia*). Individual variations within any one population of these two species seem to be roughly of the same magnitude and qualitative type. We may presume that similar mutations are appearing in each. Yet song sparrows have broken up into about 28 races on the North American continent, whereas Lincoln sparrows have divided into but 3. The Lincoln sparrow, apparently through habitat selection, adheres to a more sharply circumscribed environment than do the song sparrows, whose selecting instincts have permitted pioneering of somewhat diverse situations, thus opening up to the species new geographic areas and new possibilities of adaptational adjustment. Establishment of numerous geographically and ecologically isolated colonies of Lincoln sparrows has been thwarted by the rigid adherence to a certain type of fresh-water marsh.

The positive action of habitat selection comes about, as already implied, by providing isolation of populations within a species. In other words, if selection is not too restrictive and too constant so that exploration is prevented, pioneering of detached areas takes place. Habitat selection may then help to hold the pioneer populations from indiscriminate dispersal and hence swamping of differences arising in isolation, and/or it may itself change so that different features of habitat are perceived and a population of a new geographic area or ecologic situation is thereby held apart. The chestnut-backed chickadees of Marin County, California, which were established there by some early pioneering or dispersal, perhaps are held in isolation and their distinctiveness promoted and preserved by their habitat selection. These chickadees certainly have the ability to fly across the Golden Gate to suitable areas on the San Francisco Peninsula. They have the equipment but not the "desire," so to speak, to leave their habitat, even for a few hundred yards.

Deviations (mutations) in the instinct of habitat selec-

tion must from time to time arise. Lack's reed bunting that nested far away from a marsh may be an instance. Around San Francisco Bay, and to less extent the bays farther south on the Pacific coast, marsh or Savannah sparrows nest both in the *Salicornia* of the tidal lands and in the adjacent and different grassy uplands. One group of birds selects one situation, the other a distinctly different one. In this instance we do not know how rigid the separation of the two populations may be. But in the same habitats, about the bay, meadow mice, harvest mice and song sparrows each have populations in the *Salicornia* marsh and in the grassland, and the populations are morphologically somewhat different, indicating an effective isolation in these adjoining habitats. In the harvest mouse the forms are fully isolated, behaving as species. In all these groups of animals, and, particularly at the initial stage which seems to exist in the marsh sparrows, habitat selection figures, probably critically.

Establishment of ecologic races, as in these instances about San Francisco Bay, is actually much less common than the prevailing geographic segregation among birds and mammals. Even in these bay region races there is also something of a geographic factor, as the two environments are spaced and not extensively intermixed in any one small area. Nevertheless in geographic isolation, as has perhaps been sufficiently suggested, habitat selection functions. Rarely do we see purely ecologic races, but we may say that rarely are the geographic races purely geographic and devoid of the ecologic aspect, which may in reality have been basic.

Thus far we have discussed habitat selection as a purely instinctive affair. To neglect the learning factor would be a serious mistake, for there is much to show that within instinctive limits an individual early is impressed with its surroundings (Whitman, 1919; Lorenz, 1937), animate and otherwise, and seeks to remain with these. Habits and associations with respect to environments and particular landmarks are passed on non-

genetically from generation to generation. Cultures or societies are formed in higher vertebrates, as indeed in humans, and temporary barriers are set up. Perhaps the hill-dwelling song sparrows of San Francisco Bay do not associate with those on the salt flats, figuratively and literally on the other side of the railway tracks, because of their upbringing. In recent studies of flocking corvids this kind of situation has been stressed by Emlen (1940) and Cushing (1941) as a limiting and isolating factor in distribution. Traditional roosting places are used and learned by successive generations. Instinctive is the tendency toward gregariousness and returning to familiar habitats and roosts, but the particular societies and roosts to which each group is limited are a matter of learning. The effective breeding population, to use this term in Dobzhansky's sense, is accordingly small. Great are the possibilities of psychologic isolations, then, in animals with complex central nervous systems. To successfully understand the evolution of higher vertebrates these aspects of the natural history of each species must be fully explored.

#### LITERATURE CITED

- Benson, S. B., and Borell, A. E.  
1931. *Jour. Mamm.*, 12: 226-233.
- Cushing, J. E., Jr.  
1941. *Condor*, 43: 103-107.
- Dobzhansky, T.  
1937. "Genetics and the Origin of Species." New York: Columbia University Press.
- Emlen, J. T., Jr.  
1940. *Condor*, 42: 287-294.
- Grinnell, J.  
1928. *Univ. Calif. Chronicle*, 30: 429-450.
- Lack, D.  
1933. *Jour. Animal Ecol.*, 2: 239-262.
- Lorenz, K.  
1937. *Auk*, 54: 245-273.
- Miller, A. H., and McCabe, T. T.  
1935. *Condor*, 37, 1935: 144-160.
- Wright, S.  
1931. *Jour. Am. Stat. Soc.*, 26: Suppl., March, 201-208.
- Whitman, C. O.  
1919. *Carnegie Inst. Washington*, publ. 253, 3: 1-161.

## POLYPLOID COMPLEXES IN RELATION TO ECOLOGY AND THE HISTORY OF FLORAS

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IN the study of present-day associations of plants, one of the important problems to be solved is the origin and past history of these associations. Where did the species which form them come from, and how did they become associated? Direct evidence bearing upon this problem can sometimes be obtained from the fossil record, but this record is often fragmentary or entirely lacking, so that we must fall back upon indirect evidence. Plant geography, or the study of the present distribution of the species found in an association, together with that of their relatives, has in the past century provided such evidence in ever-increasing quantity (Fernald, 1931; Raup, 1941). The value of much of this evidence depends upon the fact that some members of any group of related modern species are old, while others have been derived in relatively recent times. In most cases the crucial question of which are the original and which the derived members of a group has been left to the subjective judgment of the plant geographer or systematic monographer. It is obvious, however, that the interpretation of the history of floras from present-day plant distribution will be much easier if we can find a criterion which makes it possible for us to tell with some degree of certainty both which are the derived members of a group of related forms and also how they have been derived. Such a criterion is provided in a large number of groups of plants by the phenomenon of polyploidy. This phenomenon, namely, the existence within groups of related species of chromosome numbers which are multiples of each other, is now well understood by cytogeneticists (Stebbins, 1940). We can therefore say with some confidence that doubling of the chromosome

number occurs frequently, and under certain circumstances may produce new vigorous, fertile, aggressive lines, while halving of the number is very rare and results in weak, sterile offspring which seldom if ever survive in nature. In any polyploid series found in nature, therefore, those members with the lowest number of chromosomes are the primitive ones, while the polyploids are derived from them. This principle leads naturally to the corollary that any flora or plant association which contains a relatively large number of diploid species is a relatively old or original one, while an association consisting largely of the polyploid members of such series has been evolved relatively recently.

The proper use of this criterion depends, of course, upon what we know about the way in which polyploid series are built up. This can be accomplished in a number of ways, but the possible types of polyploid series can be classified by the recognition of two extreme classes plus a group of intermediate types.

One extreme is the diploid species which has built up a series of autopolyploids through the direct doubling of the chromosome number without any other genetic changes having occurred. Such series are best known in experimental material such as tomatoes (Lindstrom and Humphrey, 1933), maize (Randolph, 1935), and mosses (Wettstein, 1928). During the past year I have begun to produce one in the native grass species, *Stipa lepida* Hitchc. This species has one of the lowest chromosome numbers known in *Stipa*,  $2n = 34$ . By treating with colchicine seeds of a plant from Berkeley several tetraploid and part tetraploid plants were produced. Seeds from these plants gave rise to six progenies, two consisting entirely of tetraploids with about 68 chromosomes, and four of both tetraploid and diploid plants. The data obtained on these progenies will be presented in detail elsewhere, but a few facts about them are pertinent to this discussion. In the first place, the tetraploids were all slower in growth and later in flowering than their nearest diploid relatives,

although one progeny contained tetraploids that were earlier than diploids of other progenies. In other words, chromosome doubling produced slow growth and maturation, but the same effect was produced by genic segregation. Although variation in vigor was found among both diploids and tetraploids, the latter were distinctly the more variable. Some appeared more vigorous than their diploid relatives, others less so. The greater breadth and thickness of the leaves characteristic of most tetraploids is not evident in *Stipa*. Third, the size of the floral parts is greater, and the fertility considerably reduced. Seed setting varied from about 70 per cent. to complete sterility. These characteristics are typical of autotetraploids. It is particularly interesting to note that at least in their vegetative characteristics the tetraploids show a remarkable range of variation; apparently the effects of chromosome doubling depend considerably upon the character of the original genotype.

Such autoploid series undoubtedly occur in nature. In the California flora there is a good example in *Fritillaria lanceolata* Pursh. In this case, and probably in most others, the autoploids are ecologically nearly equivalent to their diploid progenitors, and do not seem to have played an important role in the evolution or spread of the species.

At the other extreme is the case of two distantly related species which have crossed to produce a completely sterile hybrid. From this hybrid an allotetraploid has arisen, which is very distinct from either of its parents, although intermediate between them. Such a case is represented by the cultivated tobacco, *Nicotiana Tabacum* (Greenleaf, 1941). Here the systematist can recognize three distinct species, while the cytogeneticist can go farther, and explain the origin of one of them.

Between these two extremes is great middle ground of polyploid series built up from diploid species that are distinct but closely related, so that first generation hybrids between them are partly or wholly fertile. In these cases

it is often possible for the allopolyploids (or "auto-allo-polyploids" in the sense of Upcott, 1939) to cross back to their diploid parents or to autoploid derivatives of these diploids. From such secondary hybrids fertile polyploid forms may be derived which show all degrees of intergradation between the original diploids. Thus a polyploid complex is built up (Babcock and Stebbins, 1938; Stebbins, 1940). Such a complex may be pictured as a series of distinct pillars, representing the diploid forms, which support a great superstructure of intermediate polyploids. Its taxonomic complexity is obvious, and need not be emphasized here. I should like, however, to point out that here we have a great array of forms which differ in their ecological requirements as well as in their external morphology, and that the origin of most of these forms can be postulated, and tested by actual experiments.

Two examples in the western flora of such complexes, *Zauschneria* (Clausen, Keck and Hiesey, 1940) and *Crepis* (Babcock and Stebbins, 1938) have already been studied. I should like to point out a third which, judging from the preliminary data obtained, offers great possibilities, namely, *Eriogonum*. In this large western American genus ten or twelve of the perennial species have been investigated cytologically by Miss Susan Stokes (unpubl.) and nearly all have 40 chromosomes as the diploid number. Although no species with 20 chromosomes have yet been found, the numbers 18 and 22 found in the annuals suggest that 20-chromosome species do exist or have existed in the genus, so that the 40-chromosome perennials are probably tetraploids, and represent the superstructure of an ancient polyploid complex or series of complexes. In addition, the two most common Californian species, *E. latifolium* Sm. (sens. lat., incl. *E. nudum* Dougl.) and *E. fasciculatum* Benth., have built up new complexes of octoploid, 80 chromosome types which are intermediate between various ones of the tetraploids. I should like now to illustrate a part of the secondary com-

plex included by systematists in *E. fasciculatum* Benth., the common shrubby wild buckwheat of southern California. Omitting the forms from the desert areas and Arizona, which have not yet been studied, we can recognize two tetraploids. One, recognized in systematic treatments as the typical form, or subsp. *typicum* (Stokes, 1936), is a shrub with narrow, densely fascicled leaves that are generally bright green and glabrous above; glabrous involucres; and flowers slightly or not at all hairy. It is the common form near the coast about San Diego and southward for 350 miles into Lower California, extending northward in gradually decreasing abundance to the Santa Monica Mountains and the Ojai Valley. The other, subsp. *polifolium* (Benth.) Stokes (*E. polifolium* Benth.) is usually a smaller shrub, has broader, blunter, less fasciculate leaves which are grayish-pubescent on both sides; tomentose involucres; and hirsute flowers. It is characteristic of the interior of the state, being abundant along the edges of the deserts, in the drier mountains of Southern California, and extending northward along the west side of the San Joaquin Valley.

These two tetraploids are in general quite distinct from each other. Their ranges overlap only in San Diego County and perhaps Lower California, and here there is usually little difficulty in recognizing a tetraploid as either good *typicum* or good *polifolium*. Morphologically, however, they are connected by a whole series of intergrading, intermediate forms, so that the field observer gains the impression that they pass gradually into each other. Cytological examination of a considerable number of these intermediates, and measurements of the stomata and pollen of many more, has shown that they nearly all have 80 chromosomes in their somatic cells, or twice the number of subsp. *typicum* and subsp. *polifolium*. This is strong evidence that these octoploids have arisen from hybrids between the two tetraploids, through doubling of the chromosome number. The most common octoploid form is that classified as subsp. *foliolosum* (Nutt.) Stokes,

a name which for the present can conveniently be applied to the entire octoploid group. It is the common *Eriogonum* in the valleys and foothills of Southern California, away from the coast, and is the only *fasciculatum* type found in most of the area from Santa Barbara northward. The morphological characteristics and geographical ranges of the three types under discussion are shown in Figs. 1 and 2.

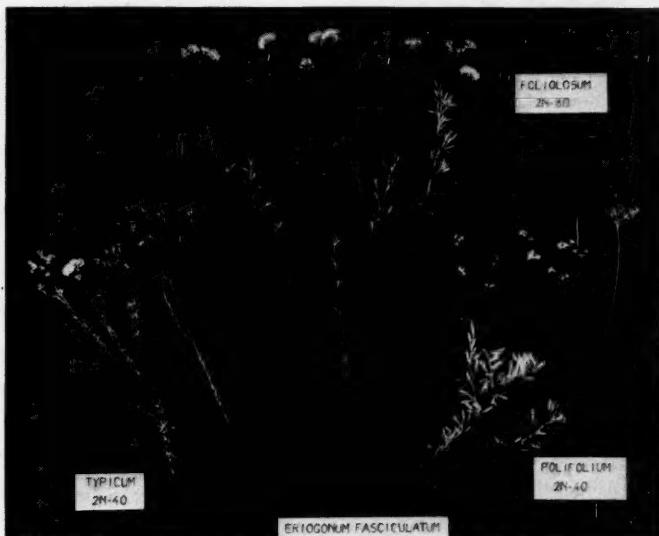


FIG. 1. Habitual characteristics of *Eriogonum fasciculatum* subsp. *typicum* (left), *polifolium* (right) and *foliolosum* (above).

Although experiments of the type described by Dr. Hiesey (Clausen, Keck and Hiesey, 1940) have not been performed on *Eriogonum*, a study of the climatic characteristics of the three forms under consideration indicates that *foliolosum* combines the physio-ecological tolerance requirements of *typicum* and *polifolium* as well as their morphological characteristics. The *typicum* tetraploids occur in an area of low rainfall, nine or less to 15 inches

per year, but one which has practically no frost and some summer moisture in the form of fog, so that the plants are active throughout the year or nearly so. Furthermore, the seasonal range of temperature is moderate; the average temperature for January in San Diego and Los Angeles is only 16° Fahrenheit lower than for July. Hence *typicum* is never exposed to extreme environmental

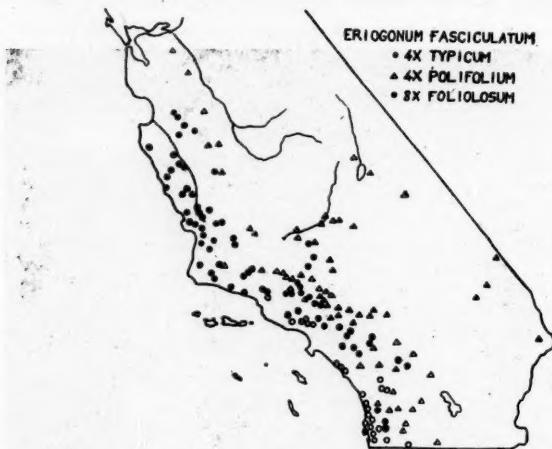


FIG. 2. Geographic distribution of *Eriogonum fasciculatum* subsp. *typicum* (open circles), *polifolium* (triangles) and *foliolosum* (solid circles).

conditions. *Polifolium*, on the other hand, occupies habitats where environmental conditions are much more extreme. The average annual precipitation varies from 4-5 inches or less in the desert areas to 25 inches in the mountains east of San Diego, but in every habitat occupied by this form there are no summer fogs or rain, so that late summer and fall conditions are very dry. Furthermore, the regions occupied by *polifolium* are subject to winter frosts and often to snowfall, so that its growing season does not begin until March, April or May, often only one or two months before all precipitation ceases for the season. The mean temperatures for January in these areas are 25 to 35 degrees Fahr. lower than those for

July, so that the seasonal variation in temperature is nearly twice as great as in the areas occupied by subsp. *typicum*.

In all these respects, *foliolosum* shows a tolerance intermediate between those of *typicum* and *polifolium*. The average annual rainfall within its range varies from 12 to 18 inches, being greater than that found in most of the area occupied by *typicum* and in much of the range of *polifolium*, but less than that in some of the mountain areas where the latter form occurs. In most of the range of subsp. *foliolosum* there is regularly some winter frost, but rarely snow, so that a mild, relatively short winter dormancy is imposed upon the plants. Summer fogs occur in some parts of its range, and summer temperatures are in general less extreme than those in the interior regions occupied by *polifolium*. The seasonal variation in temperature, 13–25 degrees Fahr., is intermediate. There is, therefore, good reason to believe that *foliolosum* has acquired combinations of the ecological tolerance requirements, as well as the morphological characteristics of *typicum* and *polifolium*.

*Eriogonum fasciculatum* subsp. *foliolosum* is, therefore, an important member of the chaparral formation of Southern California whose method of origin can be explained by a plausible hypothesis, subject to experimental proof. It is unquestionably younger than either *typicum* or *polifolium*, and should therefore occupy younger land. A study of the geological history of the areas occupied by the three forms shows that this is the case (Reed, 1933). The interior regions in which *polifolium* occurs have been for the most part continuous land since early Tertiary time or earlier. The southern coastal area, occupied by *typicum*, was raised from the sea in the late Pliocene epoch, but part of the range of this species, particularly in Lower California, is apparently on old land. *Foliolosum*, on the other hand, occupies almost exclusively areas which were under the sea in upper Miocene or Pliocene time, and much of its present range was not

available to plants until the Pleistocene epoch. This suggests that the two tetraploids under discussion already existed in the middle or latter part of the Tertiary period, but that the octoploid *foliolosum* originated and spread in accordance with the drying up of inland seas and the elevation of the land of coastal Southern California at the end of the Pliocene and the early part of the Pleistocene epochs. It was apparently a vigorous newcomer which was able by variation and natural selection to become better adapted to this new territory than either of its older, more stable progenitors.

Such a history of a polyploid complex is by no means unique. Perhaps the safest generalization that can be made about polyploids is that they are most numerous in regions that have only recently been open to colonization by plants or that have undergone great changes in their floras in recent times. Such cases as *Iris versicolor* (Anderson, 1936), *Biscutella laevigata* and its relatives (Manton, 1934, 1937), and *Crepis* (Babcock and Stebbins, 1938) may be cited as typical. It is obvious, therefore, that by discovering and proving the method of origin of the polyploid species in these recent floras we can learn much about the origin and history of the floras themselves. *Eriogonum fasciculatum* is only one out of many polyploid complexes found in the valley and foothill floras of Southern California. Faced with the interesting hypothesis presented here concerning its origin, one wonders whether similar hypotheses can be produced to explain the origin of the polyploid complexes in *Brodiaea*, *Allium*, *Arctostaphylos*, *Gilia*, *Phacelia*, *Stephanomeria* and many other genera. Turning to a broader field, one can envision the possibility of using such wide-spread holartic complexes as those in *Festuca*, *Poa*, *Salix*, *Potentilla*, *Achillea*, *Artemisia* and *Taraxacum* as keys to the history of the arctic-alpine flora, of the flora of the glaciated regions of both hemispheres, and as aids to the solution of any number of puzzling problems in plant distribution. Clearly we have here a tool of inestimable value,

but it is one which can be utilized to its full extent only through enthusiastic and whole-hearted cooperation between botanists in different parts of the world and with training in different specialties, such as taxonomy, cytology, plant geography and ecology. Let us hope that the opportunity for such cooperation will arrive before long, and that botanists will be eager to take advantage of it.

## LITERATURE CITED

- Anderson, E.  
     1936. *Ann. Mo. Bot. Gard.*, 23: 457-509.
- Babcock, E. B., and G. L. Stebbins, Jr.  
     1938. Carnegie Inst. Wash. Publ. No. 504. 200 pp.
- Clausen, J., D. D. Keck and W. M. Hiesey  
     1940. Carnegie Inst. Wash. Publ. No. 520. 452 pp.
- Fernald, M. L.  
     1931. *Rhodora*, 33: 25-62.
- Greenleaf, W.  
     1941. *Genetics*, 26: 301-324.
- Lindstrom, E. W. and L. M. Humphrey  
     1933. *Genetics*, 18: 193-207.
- Manton, I.  
     1934. *Ztschr. Ind. Abst.- u. Vererbungsl.*, 67: 41-57.  
     1937. *Ann. Bot.*, n. s. 1: 439-462.
- Randolph, L. F.  
     1935. *Jour. Agr. Res.*, 50: 591-605.
- Raup, H. M.  
     1941. *Bot. Rev.*, 7: 147-248.
- Reed, R. D.  
     1933. "Geology of California." 335 p. London.
- Stebbins, G. L., Jr.  
     1940. *AM. NAT.*, 74: 54-66.
- Stokes, S. G.  
     1936. "The Genus *Eriogonum*. A Preliminary Study based on Geographic Distribution." 124 pp. San Francisco.
- Upcott, M.  
     1939. *Jour. Genet.*, 39: 79-100.
- v. Wettstein, F.  
     1928. *Bibl. Genet.*, 10: 1-215.

## INHERITANCE IN CILIATE PROTOZOA<sup>1</sup>

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HEREDITY in ciliate Protozoa is too complex to be portrayed fully or adequately in the time at my disposal. I have therefore selected for discussion what appears to me to be the most important and interesting problem of ciliate genetics—the problem of the basis of the observed hereditary diversities. In genetics of higher organisms we have learned to interpret all hereditary diversities as due to differences in the number, arrangement or kinds of genes present, except for a few instances of plastid and other cytoplasmic differences. In the Protozoa, on the other hand, there are many observations difficult to reconcile with genic or plastid interpretations; but the great weight of evidence from higher organisms and the impracticability of carrying out the necessary genetic analysis long prevented these observations from leading to any solidly founded alternative interpretation. In recent years, however, genetic analysis has been facilitated and this has resulted in a rapidly growing body of knowledge that may lead to radically new genetic principles. I shall attempt to portray current and earlier work primarily in their relation to this.

The problem of the basis of hereditary diversities in ciliates may be studied in two kinds of material: during purely vegetative reproduction, when the genic constitution should remain constant; and at fertilization and nuclear reorganizations, when new genic combinations may be formed. In vegetative reproduction, it has been known ever since the pioneer studies of Jennings (1908) that hereditary characters ordinarily remain constant. At first all the products of uniparental reproduction were

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believed to constitute a genetically uniform clone; but later studies (Caldwell, 1933; Erdmann, 1920; Jennings, Raffel, Lynch and Sonneborn, 1932; Jollos, 1921; Kimball, 1937; Raffel, 1932a, 1932b; Sonneborn, 1935, 1937, 1939a, 1939b; Sonneborn and Lynch, 1937) showed that hereditary characters may change at nuclear reorganizations involving only one parent, and some (Caldwell, 1933; Jollos, 1921; Kimball, 1937; Sonneborn, 1937, 1939a) showed that the individuals arising at the first few fissions after both uniparental and biparental reorganizations may differ in their hereditary characters. As these reorganizations may involve fertilization (Diller, 1936; Sonneborn, 1939b) and as the immediately following fissions are not strictly vegetative (for diverse macronuclei are segregated, not divided), the clone, or group of vegetatively produced individuals, should not include them. These discoveries of hereditary diversities during uniparental reproduction thus served to call attention to the fact that we were including too much in the clone, but gave no evidence for the origin of hereditary diversities within the clone, properly conceived.

Many recorded observations do purport to show, however, that hereditary diversities may arise within such a clone. Their occurrence is almost as generally accepted as the principle of clonal uniformity itself. Yet, I believe, as I shall attempt to show, that most of the evidence for it is not critical. In much of this work the possibility that the observed diversities arose at endomixis or autogamy, and so not strictly within a clone, has not been satisfactorily excluded. This objection holds for practically all the observations on *Paramecium* except those to be mentioned later.

In most of the remaining studies, the diversities observed are not clearly hereditary.<sup>2</sup> This criticism may be

<sup>2</sup> Any definition of heredity is arbitrary and objectionable. To avoid misunderstanding, however, it is desirable to state explicitly how the term is here employed. In this paper determination by self-multiplying materials (either nuclear or non-nuclear) is considered to be the essential feature of hereditary characters; characters determined by non-multiplying materials

applied to the genetic interpretation of the well-known "life-cycle" of ciliates. Each stage in the cycle—immaturity, maturity, senescence—is marked by a number of characters persisting through many cell divisions, and so superficially appearing hereditary. Comparable changes take place during development of a multicellular organism and, while their nature is but ill understood, presumably cytoplasmic differentiations arise as a result of progressive changes in nucleo-cytoplasmic interaction. Similar processes may underlie the life cycle changes in ciliates. They may also be at the bottom of the intraclonal diversities shown in the so-called "cytoplasmic lag" effect (DeGaris, 1935; Kimball, 1939a; Sonneborn and Lynch, 1934). When hereditary characters change as a result of conjugation, autogamy or endomixis, the first individuals produced in the new clone may have the same characters as did the ancestor prior to reorganization. The new character first appears suddenly or gradually in individuals produced days or even weeks later. As not all lines of descent change simultaneously, diverse lines of descent may temporarily exist within the same clone. Until the possibility of progressive cytoplasmic changes under nuclear action is excluded, these cytoplasmic lag changes, like the life cycle changes, can hardly be considered critical evidence of intraclonal hereditary diversity.

Changes indistinguishable from life cycle changes are producible (Beers, 1933) by inadequate cultural conditions in species that manifest no such changes under favorable conditions. Other environmental actions are known (Jollos, 1921), resulting in acclimatization or increased resistance to various chemical and physical agents. Such changes are often gradually accumulated by prolonged environmental action. Though they commonly disappear at once, after removal from the inducing

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passively distributed from cell to cell are considered non-hereditary. To demonstrate that a character is hereditary it is therefore held necessary to exclude the latter possibility.

conditions, their loss also is sometimes gradual. As these gradual changes extend over many fissions, they have been considered by some to be hereditary. But this need not be if the environment produces effects on the cells more rapidly than they are being diluted by divisions. Though we must thus reject as uncritical all the types of evidence so far mentioned, there remain several studies in which the observed intraclonal diversities are probably or certainly hereditary.

The earliest apparently unobjectionable example of intraclonal hereditary diversity in ciliates is Middleton's (1915) study of the effects of selection in *Styloynchia*: lines differing in fission rate were isolated within a clone by means of repeated selections. As endomixis and autogamy are unknown in *Styloynchia*, the observed diversities appear to be intraclonal as well as hereditary.

Recently Kimball (1939b) brought to light another case of great interest. He observed that the mating types I and II in *P. aurelia*, ordinarily strictly inherited within a clone, behave very differently in certain rare clones. Such a clone includes some individuals of type I, others of type II. Ordinarily any individual, of either type, will give rise by fissions to progeny of both types. Though this looks as if the mating type is not a hereditary character in these clones, two further observations suggest otherwise. In the first place, there is some, although not perfect, correlation between the mating types of parent and offspring; usually the vegetative progeny of a cell are predominantly of the same type. Secondly, in such clones, cells occasionally arise that produce progeny of one type only; their instability has been lost; mating type is now apparently strictly inherited. The type of these stable lines, in the small number studied, was always the same as the type of the clone from which the unstable clone arose at endomixis (or autogamy), thus suggesting internal determination of the stable type.

We turn now to a class of hereditary intraclonal diversities observed by a number of investigators. These all

involve numerical or architectural changes in self-reproducing parts of the cell. The simplest kind, found by Woodruff (1931) in *P. bursaria*, by Manwell (1928) in Pleurotricha, and by others, consists simply in change of the number of nuclei per cell, and probably arose from unequal distribution of nuclei at fission. Another kind involves the production of normal single lines of descent from clones of double animals. This was found in Oxytricha by Dawson (1920), in Uroleptus by Calkins (1925), in Colpidium by Sonneborn (1932) and in other genera by others. The single animals arose by a splitting apart of the two components, or by the passage of a normal fission plane across a cleft in the anterior part of the body. These single animals reproduce true to type, as the double animals ordinarily do. Finally, the reverse phenomenon has been described; lines of double animals may arise in clones of single animals. This may happen either by a direct fusion of two animals, as in Oxytricha, or by their origin from multiple monsters, as in Colpidium. In the latter case, they arise from regions of the monster in which two sets of organelles lie parallel and similarly oriented. In all these observations there is no indication of any change in the deep-seated constitution of the cells; for the single animals that arise mechanically from doubles do not again produce doubles. Inheritance of these diversities thus appears comparable to the inheritance of chromosomal duplications or tetraploidy: rearrangements or changes in number of these structures are inherited because the structures are themselves self-reproducing.

Critical examination of the studies on inheritance during vegetative reproduction in ciliates thus leads to the conclusion that nearly all the observations held to demonstrate the origin of hereditary variations within a clone are unconvincing. Of the apparently unobjectionable observations, most involve only a relatively superficial change in number or arrangement of non-genic but self-reproducing structures. Only two observations—

the positive effects of selection in *Styloynchia* and the frequent change of hereditary characters in unstable clones of *P. aurelia*—stand out as strong evidence of changes in basic constitution within a clone. As the members of a clone ordinarily must be alike in their genes, the question raised by these two studies is whether genic changes are occurring within the clone, or whether non-genic hereditary diversities are involved. The unique position of these observations in bearing on so important a matter is a clear call for further investigation of them if we are to attain any deeper insight into this fundamental problem of heredity during vegetative reproduction.

Let us turn now to heredity in sexual reproduction where fertilization and presumably, as in higher organisms, recombinations of chromosomes and genes should be involved. Much earlier work started by Jennings (1913) on conjugation and by Erdmann (1920) on endomixis showed that hereditary diversities arose at these processes. Recent studies (Sonneborn, 1938, 1939a) on *Paramecium* have shown that such diversities are sometimes due to diversities in genes, as was generally supposed.

The most fully studied case (Sonneborn, 1938, 1939a) involves a single locus in *P. aurelia*. Individuals with only the recessive allele are always of mating type I and never can produce type II. Individuals containing the dominant allele may yield progeny of either mating type at autogamy. The characters determined by these alleles show typical Mendelian inheritance: dominants by recessives give heterozygotes; the F<sub>2</sub> gives the typical 1:2:1 ratio; and the back-cross, the 1:1 ratio. In all these crosses the two members of a pair of conjugants emerge from conjugation with identical genotypes, showing that the two pronuclei formed at the third maturation division are identical and that reduction must have occurred prior to this.

At autogamy (Sonneborn, 1939b) no genic recombin-

tion can take place in homozygous clones; but heterozygous clones are transformed invariably into homozygous ones; one half becoming recessive and one half dominant. This must mean that fertilization takes place between the products of a single reduced nucleus. In view of Diller's (1936) cytological observations, the alternative possibility—doubling of chromosome number in a single reduced nucleus—seems excluded.

If the behavior of this pair of genes turns out to be typical for ciliates, it will mean that once an individual has been through autogamy, its descendants can give rise to no other genic combinations until they conjugate with a genetically different strain, or until mutation occurs. This is presumably the basis of Jollos's (1921) observation that recombinations occur at conjugation only in stocks recently isolated from nature; for in nature crosses may occur and give heterozygotes, and when these are brought into the laboratory and cultivated as pure lines they quickly become homozygous.

The view of Jennings and others (Jennings, Raffel, Lynch and Sonneborn, 1932) that conjugation yields more variation than autogamy (endomixis) also receives some support from the newer knowledge of genic inheritance. Although in homozygous stocks neither conjugation nor autogamy can give genic variations, in heterozygous stocks autogamy yields only homozygotes, while conjugation yields in addition heterozygotes. Conjugation would thus give, for genes showing dominance, a greater number of genotypes; and, for genes not showing dominance, both more genotypes and more phenotypes. The difference in results would increase rapidly with the number of genic pairs present in heterozygous condition.

There are some hereditary diversities recently studied (Sonneborn, 1939a, 1939b) in *Paramecium* that are difficult to interpret as due to genic differences. The most fully investigated is the diversity between the mating types in the stocks of *Paramecium aurelia* that contain both mating types I and II. The basic fact here is that

the two individuals produced by the first division of an exconjugant or an exautogamous individual, may be different in mating type and give rise to clones that remain hereditarily diverse in mating type. If, as is believed, the micronuclei in these two clones are all derived by equational mitotic divisions from the same syncaryon they must be genetically alike and can not differ in the two mating types. However, the new genetic facts raise the question of whether, after all, the first and second postzygotic micronuclear divisions are indeed equational. Genetically, this can be investigated by the standard procedure of comparing the progeny of the two diverse mating types to see if they are diverse, as would be expected if the parents are genetically different. When the test is made (Sonneborn, 1937), by comparing the results of self-fertilization in the two types, it appears that they yield identical sets of progeny. At autogamy, each mating type produces both mating types and in the same proportions. Further, five successive autogamies in clones of type I produced at each autogamy the same results as in the preceding ones and the same as in five successive autogamies in clones of type II. The conclusion that the micronuclei in the two mating types in such stocks are genetically identical seems inescapable.

There remains the possibility that the macronuclei in the two mating types are genetically diverse. Again, present knowledge weighs against this, for the two new macronuclei produced in each exconjugant or post-autogamous individual are derived from divisions of the same syncaryon, presumably by equational mitoses. However, there could conceivably be a reduction or elimination of chromosomes in the development of macronuclei from micronuclei. In agreement with this, cytologists have reported extrusion of chromatin during this development. Although I at first was inclined toward this view, subsequent genetic evidence has led me to abandon it. For in the cross of homozygous stocks differing in the genes determining whether only type I or both types

may be produced, the heterozygotes should give very different results depending upon whether the macronuclei are haploid or diploid. If they are haploid, the half of the clones that get macronuclei with the recessive allele can produce only type I, while the other half will produce some clones of each type, and this should result in an excess of type I among the hybrids; whereas, if all are diploid, no such restriction to type I exists and an excess of type I is not required. Actually, groups of hybrids sometimes produce the greatest excess of *type II* ever found, 75 to 85 per cent. of the resulting clones being of this type. Reduction of the genes apparently does not take place: the macronuclei remain diploid.

Conceivably other differences between the macronuclei might determine the difference between the two mating types. The macronuclei might differ in a particular translocation or inversion with the difference in mating type a position effect; but the high frequency with which this would have to occur, its limitation to a special moment in the life history, and its dependence on the genotype make this possibility highly improbable. On the other hand, the dominant allele that permits development of either mating type may be an unstable gene mutating only in nuclei destined to develop into macronuclei and with a high frequency. Such mutations might occur in one of three ways. First, they could be from an indifferent to a differentiated condition (determining only type I or only type II). Second, they could be from either type to either type. If so, the mutations would have to occur at the same frequency in either direction, for the mating type ratio is independent of the parental type. Moreover, the assumption of an unstable gene for type II must be made in the face of evidence against the existence of any stable gene for this type. Finally, the observed effect of temperature set forth below would necessitate opposite temperature effects on the mutation rates of the two assumed alleles. The third possibility, that the micronuclear genes are always for one type and

mutate only in the anlage of the macronucleus, would involve the enormous mutation rates of 50 to 85 per cent. if the micronuclear gene is always for type I and 15 to 50 per cent. if they are always for type II. While this last possibility is the least improbable, all these attempts to interpret the difference between the mating types as due to micronuclear differences of an orthodox genetic kind involve more or less improbable assumptions.

Could cytoplasmic differences, like plastid differences in some plants, be involved in the inheritance of these characters? The earlier mentioned phenomena of cytoplasmic lag indicate that cytoplasmic differences may determine mating type for a number of fissions.

On the other hand, much evidence shows the macronucleus, not the cytoplasm, is the determinant of mating types in *P. aurelia*. For the types change only when the macronuclei are destroyed and new ones are formed, i.e., at conjugation and autogamy. As the micronuclei are also undergoing special activities at the time the macronuclei are reforming and segregating, the question might be raised as to whether the mating types are directly determined by the micronuclei, not the macronuclei. Three lines of evidence together effectively eliminate this possibility. First, two cells produced by division of one differ in mating type only when two independently formed macronuclei separate, instead of dividing; this takes place normally at the first fission after conjugation or autogamy when two new macronuclei are formed; at the second or third fission in those rarer cases when more than the two new macronuclei are formed. Second, races have been found lacking micronuclei and yet with definite mating types. Third, as will be presently described, in some lines of descent new macronuclei develop from fragments of the old one: in these reorganizations the mating type never changes, in spite of the fact that micronuclear processes, possibly even syngamy, sometimes occur. In view of these facts, the mating types can not be directly determined by the micronucleus, but must be directly under control of the macronucleus.

This macronuclear determination is affected by the temperature prevailing during conjugation or autogamy and the immediately following reorganization. The temperature effect is especially marked in variety 3, where the proportion of clones of type VI increases with temperature, though a similar relation appears to hold also in variety 1. The environmental conditions prevailing during nuclear reorganization thus appear to influence the character that will be determined by the new macronuclei. It is possible or even probable that the environment acts indirectly through the mediation of the cytoplasm, for at very low temperatures the types V and VI are not changed, both clones from each parent conjugant retaining the type of the parent, as occurs commonly at all temperatures in some crosses of types III and IV. In the inheritance of types I and II, the effect of the environment on the macronucleus—regardless of whether it operates through the cytoplasm or not—is confined to a brief sensitive developmental period and persists during vegetative reproduction.

The problem is therefore narrowed to this: the difference between the two mating types is due to a difference in their macronuclei and this is influenced by the environmental conditions prevailing at the time the macronuclei develop from micronuclei and at no later time; how then do the macronuclei differ? In the preceding discussion the improbability of any genic difference was pointed out, but no more probable interpretation is apparent.

A very different kind of inheritance has just come to light in my current studies on *P. aurelia*. A previously undescribed method of nuclear reorganization has been found both in single animals, like autogamy, and in paired animals, like conjugation. The micronuclei may or may not be present, but they do not give rise to macronuclei. Instead, new macronuclei develop from the fragments of the old macronucleus which has disintegrated, as in conjugation and autogamy, by unravelling into skeins and breaking up into spherical pieces. Each of the many

spherical fragments develops into a new macronucleus and these are segregated at subsequent fissions until only one is present in each individual. This shows that the macronucleus is compound, for each fragment contains all that is required for normal macronuclear functioning.

The mating type of an animal never changes at this process of macronuclear regeneration, in contrast to the regular changes occurring at normal autogamy and conjugation. On the other hand, a whole complex of new characters always appears whenever macronuclear regeneration has occurred. The animals become smaller and of different form; they reproduce more slowly; they are less viable and die out after a period of weeks or months; new reorganizations of the same kind follow at very short intervals; the mating reaction is unusually intense; and the micronuclei often disappear. This new reorganization process and its regular consequences have been observed in several races; in certain lines of descent it is the only reorganization process that occurs. We have here therefore a definite complex of hereditary characters repeatedly appearing as a consequence of a simple macronuclear regeneration, presumably involving no genic change whatever. I find in the literature a number of accounts of this same complex of characters appearing under conditions interpreted as frequent mutations or genetic variation at endomixis; but it now appears that these may be misinterpretations resulting from inadequate knowledge of the cytological processes involved. What we have essentially is a reorganization that is purely vegetative, not involving the formation of genetically different macronuclei or of new clones, but illustrating hereditary diversity within what appears to be a genetically uniform clone.

A number of observations in the literature, viewed in relation to the newer work just set forth, will illustrate further the difficulties involved in attempting to extend to such situations in the ciliates the principles of genetics that apply so generally to higher organisms.

After long-continued inbreeding, races studied by Jennings (1913) continued to give hereditary variations at conjugation. His suggestion that "Mendelian recombinations might not be the whole of the matter" is now strengthened; for our present knowledge of the genetic consequences of autogamy makes it practically certain that his races did quickly become homozygous for all their genes. Similarly, the paramecia used in the later studies of Raffel (1932b), of Sonneborn and Lynch (1934) and of others were also probably homozygous. It would appear therefore that the many hereditary diversities found in all these studies must have been due either to mutations or to some non-genic differences.

Another class of observations includes the frequent exceptions to Jennings' principle of biparental inheritance. Jennings (1913) discovered long ago that after two individuals conjugate they tend to produce similar clones. He designated this relation as biparental inheritance. The similarity of the two exconjugant clones was interpreted as indicating they had identical genes; and the identity in genes was the result of the formation of the gamete nuclei from a haploid nucleus produced by chromosome reduction at the first two maturation divisions. The recent work (Sonneborn, 1938, 1939a, 1939b) on genic inheritance in *P. aurelia* is a striking proof of the correctness of this view.

Many studies have shown, however, that in certain characters the two conjugants of a pair frequently give rise to diverse clones. This has again been confirmed recently: Jennings (1939a, 1939b) found it in about one eighth of the mate-pairs in *P. bursaria*; I (1939a) have found that mating types in *P. aurelia* are invariably diverse in the progeny of mate pairs in certain crosses and under certain conditions, while under other conditions the same characters show similarity in the two mate-progenies no more often than expected by chance. Applying the same reasoning as before and still assuming genic determination of the characters, some students

(Raffel, 1933) of the problem have suggested or concluded that differences between the progeny of mates must be due to differences between their gamete nuclei resulting from reduction at the third maturation division. In *P. aurelia* evidence I have previously set forth shows that the known gene pair is always reduced prior to this. As there is at present no proof of third division reduction in any case and as the evidence demonstrates earlier reduction in the only known case, it would now appear that the weight of existing evidence points not to third division reduction, but to some other cause as the usual basis of differences between mate progenies. Whether this other cause is again mutation or some non-genic mechanism can not at present be decided.<sup>3</sup>

There remains for consideration one great class of observations in ciliate genetics. Jollos (1921), in one of the most intensive and extensive series of studies in ciliate literature, arrived at the conclusion that many characters persisting through hundreds of fissions and even sometimes through autogamies (endomixes) and conjugation were not genic but due to the long lasting effects of environmental conditions on the plasma, effects that always eventually wear off and disappear under action of the unaltered genes. This class of characters he calls "Dauermodifikationen." In some respects these phenomena are similar to the inheritance or mating types in stocks of variety 1 of *P. aurelia* that produce both of them. In both cases, the hereditary differences may not be due to genic differences. In both, the same environmental conditions determine the production of the characters in some races but not in others. Finally, the

<sup>3</sup> Genetic experiments performed by the author since this paper was written have shown that in *P. aurelia* some of these differences between mate-progenies are due to the occasional failure of "conjugants" to exchange gamete nuclei, in agreement with previous cytological observations on other species of *Paramecium* by Diller and by Wichterman. However, it seems unlikely that all such differences will be found to be due to this, for many have been observed in conjugation between presumably identical homozygotes.

mating types, like Dauermodifikationen, may change at autogamy and conjugation.

But in other respects, the mating types differ radically from Dauermodifikationen, as portrayed by Jollos. Dauermodifikationen are producible within a clone, presumably at any time, while mating type changes occur only at nuclear reorganizations. Dauermodifikationen disappear eventually during the passage of fissions alone, and gradually, in a series of step-like stages; mating types persist indefinitely during fissions and normally change only at reorganizations and not in step-like gradations. Dauermodifikationen may persist through several nuclear reorganizations in all lines of descent before they disappear in all; mating types never show this behavior. Change of Dauermodifikationen is accelerated by frequent change of environmental conditions; there is no evidence that anything but nuclear reorganization can normally change mating types.

Dauermodifikationen are interpreted by Jollos as plasmatic and not genic, though others (Raffel, 1932b) have attempted to interpret them as gene mutations. It would be desirable to reinvestigate these phenomena employing the methods of genic analysis now available; but Jollos (1934) has already pointed out how highly improbable the mutation interpretation is.

I have reviewed in this paper some situations in ciliate genetics in which typical genic inheritance is unquestionably involved; but I have also attempted to set forth a number of situations, including by far the greatest part of what is known about ciliate genetics, which are extremely difficult to interpret along orthodox genic lines: the existence of hereditary differences within a clone; the inheritance of mating type in stocks of *Paramecium aurelia* that contain both types I and II; the inheritance of a complex of characters associated with macronuclear regeneration; the failure to obtain by inbreeding clones that remain constant at conjugation; the production of

hereditary diversities of many kinds at conjugation and autogamy in material that should be homozygous; the production of diverse progenies from two individuals that have conjugated with each other and should be genetically alike; and the great class of Dauermodifikationen presumed to be plasmatically determined. Attempts have been made, notably by Raffel, to interpret many of these phenomena in terms of mutations; similar interpretations can be made for all of them. Such interpretations are however purely formal and there is no genetic situation, however bizarre it may be, that can not be "explained" by mutations if appropriate assumptions are made. To treat all the phenomena discussed here in this way would require many and often highly improbable assumptions. Yet these may turn out to be justified. They may be no more remarkable than the macronucleus, uniquely confined to ciliates, which may present especially in its early development conditions highly favorable to mutation. On the other hand, as Jollos maintains, non-genic factors may be involved. One of the main tasks students of the genetics of ciliates face is the solution of this difficult but important problem.

#### LITERATURE CITED

- Beers, C. D.  
1933. *Arch. f. Protistenk.*, 79: 101-118.
- Caldwell, L.  
1933. *Jour. Exp. Zool.*, 66: 371-407.
- Calkins, G. N.  
1925. *Jour. Exp. Zool.*, 41: 191-213.
- Dawson, J. A.  
1920. *Jour. Exp. Zool.*, 30: 129-157.
- DeGaris, C. F.  
1935. *Jour. Exp. Zool.*, 71: 209-256.
- Diller, W. F.  
1936. *Jour. Morph.*, 59: 11-67.
- Erdmann, R.  
1920. *Arch. f. Entw.*, 46: 85-148.
- Jennings, H. S.  
1908. *Proc. Am. Phil. Soc.*, 47: 393-546.  
1913. *Jour. Exp. Zool.*, 14: 279-391.  
1939a. *AM. NAT.*, 73: 414-431.  
1939b. *Gen.*, 24: 202-233.

- Jennings, H. S., D. Raffel, R. S. Lynch and T. M. Sonneborn  
1932. *Jour. Exp. Zool.*, 62: 363-408.
- Jollos, V.  
1921. *Arch. f. Protistenk.*, 43: 1-222.  
1934. *Arch. f. Protistenk.*, 83: 197-219.
- Kimball, R. F.  
1937. *Proc. Nat. Acad. Sci.*, 23: 469-474.  
1939a. *Gen.*, 24: 49-58.  
1939b. *Jour. Exp. Zool.*, 81: 165-179.
- Manwell, R. D.  
1928. *Biol. Bull.*, 55: 433-439.
- Middleton, A. R.  
1915. *Jour. Exp. Zool.*, 19: 451-503.
- Raffel, D.  
1932a. *Biol. Bull.*, 62: 244-257.  
1932b. *Jour. Exp. Zool.*, 63: 371-412.  
1933. *Jour. Exp. Zool.*, 66: 89-123.
- Sonneborn, T. M.  
1932. *Biol. Bull.*, 63: 187-211.  
1935. *Anat. Rec.*, 64 (suppl. 1): 103.  
1937. *Proc. Nat. Acad. Sci.*, 23: 378-385.  
1938. *Science*, 88: 503.  
1939a. *AM. NAT.*, 73: 390-413.  
1939b. *Anat. Rec.*, 75 (suppl. 1): 85.
- Sonneborn, T. M., and R. S. Lynch  
1934. *Jour. Exp. Zool.*, 67: 1-72.  
1937. *Gen.*, 22: 284-296.
- Woodruff, L. L.  
1931. *Quart. Jour. Micr. Sci.*, 74: 537-545.

## GEOGRAPHIC VARIATION IN PARAMECIUM AND THE RÔLE OF STABILIZING SELECTION IN THE ORIGIN OF GEOGRAPHIC DIFFERENCES

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### INTRODUCTION

THE possible causes of geographic variation in animals were for the first time clearly brought to light by Charles Darwin, when he wrote: "It is well known to furriers that animals of the same species have thicker and better fur the farther north they live; but who can tell how much of this difference may be due to the warmest-clad individuals having been favored and preserved during many generations, and how much to the action of the severe climate, for it would appear that climate has some direct action on the hair of our domestic quadrupeds." This question could hardly be adequately answered even at this time. We are not sufficiently informed on the part played in geographic differences by the somatic modifications due to direct effect of geographic environment, and on the other hand of the possible part played by natural selection of casual genotypic variations, strengthening the external expression of non-hereditary somatic modifications (stabilizing selection sensu, Schmalhausen, 1939).

It seems promising to analyze such relations in great detail for the case of geographic variation in Protozoa, which are in some respects particularly appropriate for a work of this kind. The existence of orderly geographic differences in these unicellular organisms is very probable for *a priori* reasons. Moreover, Mishustin (1939) has recently shown on *Bacillus mycoides*, isolated from soils of various localities, the existence of stable hereditary differences in the temperature optima of development, which are directly related to the temperature conditions of natural habitats of these bacteria.

The present work is limited to the analysis of geographic variation in three species of the genus *Paramecium* (*P. aurelia*, *P. caudatum* and *P. bursaria*). This study revealed the fact that the northern Paramecia are larger than the southern one (Bergmann's rule of geographic variation), and that these differences are hereditary. Experiments on crossing different geographic forms with each other have shown the orderly differences in their genotypes. Hereditary distinctions were also found in the optimal temperatures for multiplication of Paramecia from various localities. Further studies have also led us to conclude that the origin of hereditary differences of this kind can be easily observed under controlled change of laboratory conditions. Hereditary differences appear here by the way of natural selection of casual inherent variations arising at the time of sexual process (conjugation), whenever the latter strengthen the primary non-hereditary environmental modifications (the principle of stabilizing selection).

#### MATERIAL AND METHODS

The following clones of *Paramecium* were used in the present study:

(1) *P. bursaria*: Southern (from the environs of Odessa)—4 clones isolated from natural conditions; Moscow (from the railway station Kossino)—5 clones; Northern (station Pojagonda on the shore of the White Sea)—3 clones.

(2) *P. caudatum*: Southern (Simpheropol in Crimea)—2 clones; Moscow (various localities)—5 clones.

(3) *P. aurelia*: Southern (various localities in Crimea)—4 clones; Moscow (various localities)—2 clones.

Paramecia were cultivated on the medium of the following composition. Salt solution:  $\text{Ca}(\text{NO}_3)_2$ —30 mg;  $\text{KNO}_3$ —10 mg;  $\text{MgSO}_4$ —10 mg;  $\text{H}_2\text{O}$  (bi-distilled from glass)—500 cc. Two platinum loops of *Bacillus subtilis* and six loops of *Torula utilis* (which were previously grown on solid media in the Petri dishes) were added to

each 100 cc of the salt solution. Reinoculations of Paramecia were made once in six days. Fifty specimens of *P. caudatum* or *P. aurelia* were put into each 5 cc of the fresh medium. In *P. bursaria* 60 to 70 individuals were transferred to 3 cc of the new liquid.

The method of study of the temperature optima of division rate was as follows. Paramecia were first standardized for experimental purposes. To that end 50 individuals of each clone were placed into 5 cc of the nutritive medium for 24 hours. On the following day Paramecia were inoculated into depression slides or small tubes (for *P. bursaria*), containing nutritive liquid, by two individuals in each. This material was put into moist chambers and kept in thermostats at various temperatures for one (*P. caudatum* and *P. aurelia*) or two days (*P. bursaria*), and then the number of individuals was counted.

The material for measurements of body size was standardized in the same way. Paramecia were fixed by Schaudin's liquid and immediately measured under the microscope.

Experiments on crossing with each other of separate clones of *P. bursaria* of different geographic origin were arranged as follows. We were primarily interested in the quantitative evaluation of mortality among ex-conjugants. It is known that Paramecia of opposite mating types do not cross when taken from the fresh overfed cultures (Jennings, 1939). To bring the material into the proper physiological condition for conjugation, we kept the clones in the thermostat with a glass wall at 16° (night) and 20° (day temperatures) for 1½ months. Paramecia were fed from time to time by adding food organisms by a platinum loop. The feeding was abandoned on 8 to 10 days before crossing the infusoria.

#### TEMPERATURE OPTIMA OF DIVISION RATE

The object of this work was to find out the temperature at which the division-rate is greatest. Each experiment

was usually performed at the following temperatures: 17°, 20°, 23°, 26°, 29°, 32°, 35° C. In *P. caudatum* 20 experiments were made with 5 Moscow clones and 12 experiments with 2 Southern clones. In *P. aurelia* there were 26 experiments with 4 Southern clones and 16 experiments with 2 Moscow clones. In *P. bursaria* 11 experiments deal with 4 Southern clones, 9 experiments with 3 Moscow clones and 9 experiments with 3 Northern clones.

In each separate experiment the optimal temperature for division rate was recorded and the data obtained were treated statistically. The results of this work are presented in Table 1 and Fig. 1.

TABLE 1  
TEMPERATURE OPTIMA OF DIVISION RATE IN DIFFERENT SPECIES OF THE GENUS  
PARAMECIUM, COLLECTED IN VARIOUS LOCALITIES. OPTIMA ARE  
EXPRESSED IN DEGREES CENTIGRADE

Species	North	Moscow	South
<i>P. bursaria</i> .....	23.96 ± 0.30	28.41 ± 0.18	28.94 ± 0.14
<i>P. aurelia</i> .....	.....	29.51 ± 0.35	31.35 ± 0.22
<i>P. caudatum</i> .....	.....	29.44 ± 0.23	30.04 ± 0.53

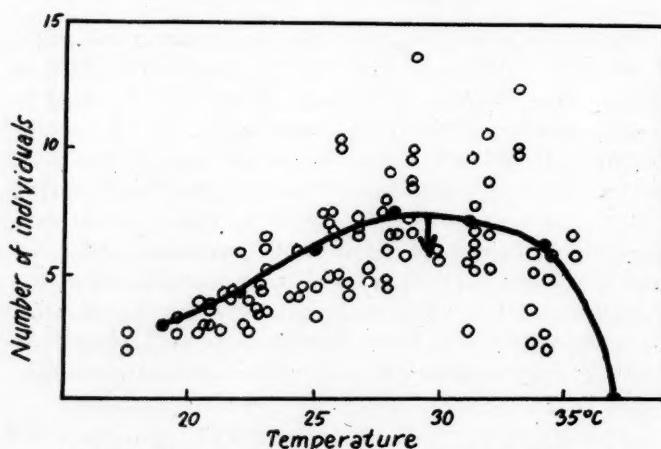


FIG. 1. Optimal temperature for multiplication in two Moscow clones of *Paramecium aurelia*. The white circles are the averages for all the data available.

It is clear that Northern Paramecia possess lower temperature optima of division-rate than the Southern ones. These differences are particularly distinct in *P. bursaria*; they are also statistically significant in *P. aurelia*. Only in *P. caudatum* in the sample of clones studied the difference between Northern and Southern varieties was not found to be statistically significant.

The experiments reported in Table 1 were made not less than five months since the infusoria were isolated from nature and kept under uniform laboratory conditions. Hundreds of vegetative divisions were performed and (in *P. aurelia*, at least) endomictic processes recorded. Hence it is concluded that the differences between Southern and Northern varieties of Paramecia in the temperature optima of division rate are hereditary.

It is remarkable that temperature optima for multiplication in Northern, Moscow and Southern varieties of *P. bursaria* are closely correlated with the summer (July-August) temperatures of the localities from which they originate (Fig. 2). This picture is closely similar to that reported by Mishustin (1939) for *Bacillus mycoides*.

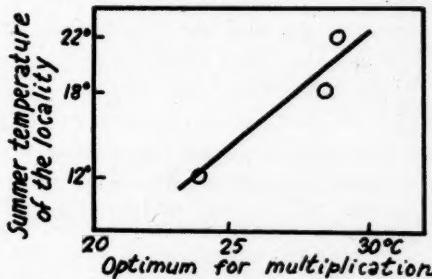


FIG. 2. The relation of the optimal temperature for multiplication of *Paramecium bursaria* to the summer temperature of the locality from which it originates.

#### GEOGRAPHIC VARIATION OF BODY-SIZE IN *P. BURSARIA*

Measurements of length and width of the body in various clones of *P. bursaria* of different geographic

origin show a regular decrease of the size of this infusoria from north to south. We have measured 60 individuals of each clone under each of the temperatures employed, and by multiplication of half-length by half-width calculated the surface of the body. The results obtained are presented graphically in Fig. 3.

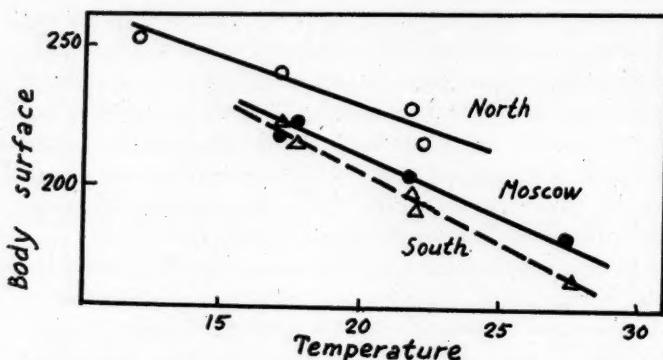


FIG. 3. The effect of temperature of cultivation upon body-surface in various geographic forms of *Paramecium bursaria*.

It is justifiable to conclude that the Northern clones are larger in the average, and the Southern clones are smaller in the average than that collected in the environs of Moscow. These distinctions are retained under different temperatures of cultivation, and as far as the whole experiment was made not less than five months since the isolation of infusoria from the conditions of nature, it is clear that geographic differences in body-size of Paramecia are hereditary.

In this connection it is important to record that modifications of body-size in *P. bursaria*, which are due to the effect of changed temperature of cultivation upon the genotypically homogeneous clones of infusoria, are not transmitted to offspring, and readily disappear with the returning of infusoria into the initial conditions of breeding. This point is proved by the following experiment. Paramecia of three Moscow and four Southern clones were

kept in pure cultures for a month under different temperatures, where they acquired some differences in body-surface. It turned out that "warm" Paramecia ( $21.9^{\circ}$  C) were by 11.1 per cent. smaller than the "cold" ones ( $17.7^{\circ}$ ). They were then placed into identical temperature conditions ( $18.3^{\circ}$  C), and dwelt there for another month. The acquired temperature differences in body-size were found practically disappeared at that time (a similar picture was recorded by Olifan, 1935, in *P. caudatum*). At the same time the differences of body-surface due to different geographic origin of infusoria attained in this experiment on the first month of cultivation 10.75 per cent., and on the second month 10.15 per cent.

It is important to note here that hereditary geographic differences in body size of *P. bursaria* go in the direction similar with that of non-hereditary modifications produced by temperature variation. This point is again presented in Fig. 3. When one compares differences of body-surface in Northern, Southern and Moscow clones of *P. bursaria*, as observed under temperatures typical for their natural habitats, with such bodily differences as can be attained by the way of temperature modification in each of geographic forms, one necessarily concludes that inherent geographic diversities in body surface represent somatically a kind of strong quantitative increase of the non-hereditary temperature modification.

#### CROSSING OF DIVERSE CLONES OF *P. BURSARIA* WITH EACH OTHER

Experiments on conjugation between different clones of *P. bursaria* have shown that in all cases some percentage of exconjugants was inviable. Moscow clones were crossed with each other, Moscow with Southern, Moscow with Northern and Southern with Northern clones. Conjugants and subsequently exconjugants were isolated into small glass dishes kept in moist chambers at  $17^{\circ}$  C, and on 6th to 8th days since the completion of conjugation it was recorded how many of isolated excon-

jugants multiplied into new vigorous clones, and how many of them perished or stopped dividing. The percentage of unviable exconjugants varied with each pair of clones crossed, but the average figures showed a characteristic regularity.

The least mortality is observed after crossing Moscow clones between each other. The average percentage of unviable individuals rises somewhat in the cross Moscow by South, and attains highest values in the crosses Moscow by North and North by South. The geographic differences in percentages of unviable exconjugants are statistically significant, as follows from Table 2.

TABLE 2  
PER CENT. OF UNVIABLE EXCONJUGANTS AFTER CROSSING THE CLONES OF  
*P. BURSARIA* OF DIFFERENT GEOGRAPHIC ORIGIN

Crossing	Per cent. of unviable exconjugants	Excess of exconjugant mortality over that recorded for the cross Moscow by Moscow
Moscow by Moscow .....	33.7 ± 2.08	
Moscow by South .....	48.4 ± 2.12	14.7 ± 2.97
Moscow by North .....	89.0 ± 1.43	55.3 ± 2.52
North by South .....	76.8 ± 1.84	43.1 ± 2.78

In accordance with current views, the exconjugant mortality taking place in all the infusoria possessing a very great number of chromosomes, depends upon purely genetic causes. It is due to chance misdistributions of hereditary material at the time of sexual process, which produce unviable individuals (Jennings, 1929). The rise of non-viability in hybrids of different geographic forms testifies consequently the increase of chromosomal-genic incongruity of their genomes (Timofeeff-Ressovsky, 1939), and can be used as a measure of the latter.

We are therefore led to conclude that the incongruity of genomes of different clones of *Paramecia* rises in proportion to geographic distance between the habitats of these clones. These relations are closely similar to those which were recently recorded for insects. Pictet (1936) states that the viability of the hybrids between the moths

*Lasiocampa quercus* from different localities is inversely proportional to the distance between the localities. Similar results have been obtained by him in another moth, *Nemeophila plantaginis*. These observations have led Dobzhansky (1937) to suggest that genetic isolation may in general represent a concomitant of the genetic differentiation of separate populations.

In relation to the problem of geographic variation of Paramecia, the data concerning non-viability of hybrids possess some special significance. We have recorded above hereditary geographic distinctions in body-surface and division-rate of *P. bursaria*. It is a question whether the causes of these inherent somatic diversities are localized in cytoplasm or in the nuclei of infusoria. By comparing non-viability of hybrids with the division-rate and body-size of *P. bursaria*, one concludes that the degree of diversity of somatic characters in geographic forms is approximately proportional to the degree of diversity of their genomes, as measured by the percentage of non-viability of hybrids. These observations suggest that geographic differences in Paramecia depend upon genic diversities, in the same way as it takes place in other animals (*cf.* Sumner, 1932).

#### THE ORIGIN OF GEOGRAPHIC DIFFERENCES

It is evident that geographic variation of body-size in *P. bursaria* conforms to the so-called Bergmann's rule, which predicts the increase of bodily dimensions to the north. What is the probable origin of these inherent geographic diversities in body-size, which go in the direction similar to that presented by non-hereditary temperature modifications?

In order to elucidate this point an analysis was made of the possible part played in the origin of geographic diversities by the natural selection of chance hereditary variations arising through conjugations. Conjugating pairs of two Moscow clones of *P. bursaria* (1A and 2A)

were placed into two temperatures, 13.4° C and 25.4° C, by 50 pairs into each 2 cc of the nutritive medium of Beers. For controls were used pure clones 1A and 2A in the same temperatures and densities. Paramecia were bred in these conditions for two months, with re-inoculation of 50 individuals into fresh medium, once in six days, and then measured. The number of measurements was 50 throughout.

If in mixed cultures among progeny of exconjugants there were no natural selection, the average body surface of individuals from such cultures should be equal to the average surface of the two ancestral clones. This point is proved by special tests recently performed by Gause (1940). Experiments show, however, that in low tem-

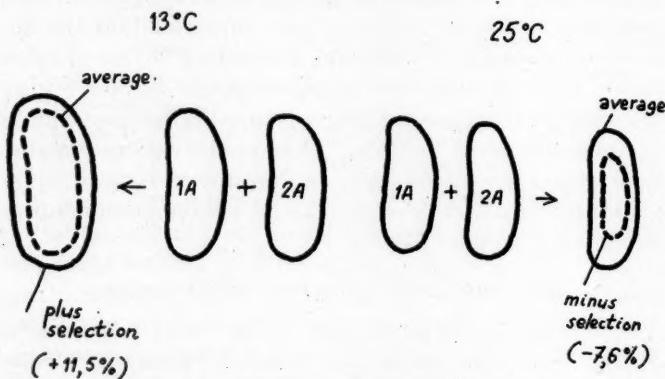


FIG. 4. The direction of natural selection for body-size in *Paramecium bursaria*, bred under different temperature conditions.

peratures the survived progeny of exconjugants in mixed cultures is by 11.5 per cent. larger and in high temperature by 7.6 per cent. smaller than the average of ancestral clones, living under the same temperature conditions in pure cultures and yielding usual temperature modifications. Hence it is reasonable to conclude that the new biotypes casually arising at the time of recombination of

hereditary material in the sexual process are of importance for natural selection. At lower temperatures the advantage belongs to larger forms, whereas at higher temperatures these are the smaller biotypes which are advantageous (Fig. 4). Natural selection of casual genotypic variations works here towards intensification of somatic changes which are primarily produced by the way of non-hereditary modifications. The same results have recently been reported by Gause (1940) in the work with *Euplotes*. It is probable that the natural selection of this kind (stabilizing selection sensu, Schmalhausen, 1939) is responsible for the origin of inherent geographic diversities similar to non-hereditary modifications, as observed in Paramecia.

#### SUMMARY

Temperature optima of division rate are lower in Northern and higher in Southern clones of *Paramecium aurelia* and *P. bursaria*. Bodily dimensions of *P. bursaria* distinctly decrease from north to south. These differences are hereditary, and they are also closely correlated with the percentage of non-viability of hybrids, which increases in proportion to somatic differences. Inherent geographic diversities of body-size in *P. bursaria* reminds somatically of temperature modifications. Experiments have shown, however, that such modifications in *P. bursaria* are not hereditary. At the same time we easily observed natural selection of casual inherent variations which strengthen the somatic effect of temperature modifications (stabilizing selection sensu, Schmalhausen). It is probable that selection of this kind is responsible for the origin of inherent geographic diversities similar to non-hereditary modifications, as observed in Paramecia.

#### LITERATURE CITED

- Darwin, Ch.  
1859. "The Origin of Species." London.  
Dobzhansky, Th.  
1937. "Genetics and the Origin of Species." New York.

- Gause, G. F.  
1940. *Zool. Zhurn.*, 19 (Russian).
- Hesse, R. W. Allee and K. Schmidt  
1937. "Ecological Animal Geography." New York.
- Jennings, H. S.  
1929. Genetics of Protozoa. "Bibliogr. Genetica," 5.  
1939. *AM. NAT.*, 73: 414.
- Mishustin, E. N.  
1939. *Priroda*, 4 (Russian).
- Olifan, W.  
1935. *Biol. Zhurn.*, 4 (Russian).
- Pictet, A.  
1936. Mem. Mus. Hist. Nat. Belgique. Ser. 2. No. 3.
- Schmalhausen, I.  
1939. "Ways and Rules of Evolutionary Process." Moscow (Russian).
- Sumner, F.  
1932. "Bibliogr. Genetica," 9.
- Timofeeff-Ressovsky, N.  
1939. "Verhandl. Deutsch. Zool. Ges.," p. 157.

## THE ACCESSORY REPRODUCTIVE TRACT IN MAMMALIAN TRUE HERMAPHRODITES, AN EFFECT OF POSITION

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THE question of the origin of true hermaphroditism in mammals is one which has attracted a great deal of attention and, as yet, no complete explanation has been found for its occurrence. The effects of the gonads upon the development of the Müllerian and Wolffian tracts in such cases are no less interesting, especially as they have a bearing upon the unilateral development of the Müllerian ducts in the female bird. Why, if hormones from the functional gonad are circulating, are not both Müllerian ducts developed in the bird, and why do we find gynandromorphic forms in mammals? A survey of the literature on true hermaphroditism in mammals has provided a partial answer to these questions. There is a local effect upon the development of the duct systems which depends upon the nature of the proximal gonad and which appears to be weakening as evolution proceeds. However, it is still strongly active even in the primate.

Krediet (1931), after examining several cases of true hermaphroditism in swine and comparing his observations with published descriptions of the condition in swine and man, has suggested that cases of true hermaphroditism may be divided into two categories:

(a) Cases in which the accessory genitalia of one sex are found on one side, corresponding to the sex of the gonad, with gonad and accessories of the other sex on the other side. These are described as gynandromorphs or space ("raum") hermaphrodites.

(b) Cases in which the accessory organs of one sex are more or less fully developed on both sides. Usually the female genitalia are the more fully developed. Some

accessory organs of the opposite sex are also present. These are described as time intersexes or hermaphrodites.

Krediet was not satisfied with the view that these two types are inherently different. He considers that ovo-testes may have been present originally in all with a degeneration of either the ovarian or testicular portions. This would place both forms in the category of time intersexes.

The classification "gynandromorph" for the type with laterally different accessory sex organs supposes that the cells on one side of the body have two X chromosomes, and those on the other one X chromosome. This seems to be true for insects, where there is no hormone control. But the inherent difficulty in accepting this view for vertebrates without some modification is that in the embryo of either sex Wolffian and Müllerian ducts are present. These develop or atrophy according to the type (male or female) of hormone produced by the gonad. Accordingly, one would expect that either the Wolffian or Müllerian ducts of each side would develop or that both would develop on each side. This is what is found in the "time" intersexes, but even here the development is not complete. The gynandromorph, or space intersex, is with present views theoretically impossible in mammals, since the unilateral development of accessory organs should not occur if the hormonal influence is the only one.

In most normal female birds the Müllerian structures are fully developed only on the left, the side on which the gonad develops. On the right with an undeveloped gonad the Müllerian duct remains rudimentary. Clearly, the position of the gonad which is developing influences the Müllerian development, possibly by bringing the tract to a state of development at which the hormone may act. Gynandromorphic mammalian forms are probably influenced in the same way so that the presence of ovary on one side brings the Müllerian duct of this side to a responsive condition. The presence of testis on the other side possibly acts similarly to bring the Wolffian duct of

that side to a responsive condition. Lillie's (1931) view that one side of the body, the side which is hypertrophied, has a higher threshold for hormone action is valid for plumage pattern in gynandromorphic birds, but, as he has pointed out, the gonadic constitution and plumage pattern do not always correspond. We might assume that the difference in the gonads in gynandromorphs is due to the presence or absence of the second X chromosome on one side or other of the animal, leaving, as Lillie did, the differences in plumage pattern to differences in the rate of growth on the two sides. But with this addition, the hypothesis does not fit the case of the normal female bird. It must be pointed out, however, that no one has yet demonstrated the necessary difference in chromosome content of the two sides of the body in the gynandromorphs. Moreover, both Müllerian and Wolffian ducts are present in the embryos of either sex.

Wiesner (1934-5) has shown that when day-old male rats are castrated, the male accessory organs fail to develop, but that in day-old ovariectomized rats the female accessories continue their prepubertal development. Androgens are effective on the male accessories of these rats but estrogens are not. This shows that there is a difference in the behavior of Wolffian and Müllerian structures under experimental conditions. It does not explain all the differences for which we have postulated a local effect, but it does afford an experimental confirmation for our conclusion that the male and female accessory organs differ in their response to their environment.

Our suggestion that the accessory sex organs of hermaphroditic mammalian forms are influenced in development by the nature of the gonad on the same side needs amplification. With this object in view, we have surveyed the literature critically and now give the results of the survey, species by species. We think that the literature confirms our suggestion, and also that it is possible to make some generalizations on the nature of the position effects. They vary according to the zoological standing

of the species, or perhaps according to the nature of the normal uterus.

#### A. RODENTIA

*Mus musculus*. Three cases have been recorded. One of these is completely gynandromorphic. There is an ovary on the left and a testis on the right side. The accessory structures correspond entirely to the gonad. In the second case the accessory organs are entirely female, while the right gonad is an ovary and the left a testis. In the third case the testis is on the left side. On this side there is a small truncated uterus without an oviduct. The male accessories are normal. On the ovarian side the accessories are entirely female.

*Mus rattus*. Two unpublished cases (quoted by the permission of Dr. R. O. Greep).

Case 1: Testis with male accessories on the left and ovary on the right. On the left side the male accessories are normal. A uterus is present on the ovarian side with an oviduct ending blindly. Male accessories are normal on this side.

Case 2: Ovotestis on the right with normal male accessories and a uterus with a blind oviduct. A testis is present on the left side with male accessories but no female accessories.

*Microtus pennsylvanicus*. One case, completely gynandromorphic.

*Citellus tridecemlineatus*. Two cases, both with ovotestis on each side. Normal male accessories on each side. Corpora uteri and horns normal on each side. Oviducts normal on left, but interrupted in the middle on the right side in each case.

*Cavia cobaya*. One case, completely gynandromorphic.

All the cases which might be described as gynandromorphs have occurred in rodents. We thought at first that it was a peculiarity associated with the duplex uterus, but the gynandromorphic guinea pig and the presence of male accessories on the ovarian side in Greep's rat

(Case 1) do not bear this out. The gynandromorphic condition may, however, be a peculiarity of the rodents.

#### B. INSECTIVORA

*Talpa europaea*. One case. An ovotestis was present on each side. The specimen was incomplete. For this paper we may note that on the right side a vas deferens was present. There was also a rudimentary oviduct on the same side.

#### C. CARNIVORA

*Felis domesticus*. One case. Ovotestis on the right with uterus and oviduct but no epididymis or vas deferens. On the left side, a testis with epididymis and vas deferens but no uterus or oviduct.

#### D. UNGULATA

*Bos taurus*. Four cases.

Case 1: Ovary on right with uterus and oviduct (normal) no male structures described. On the left a testis with an epididymis and an oviduct which was blind at the ovarian end.

Case 2: Testis on right with epididymis and vas deferens, also a uterus and an oviduct without infundibulum. An ovary on the left with normal male and female accessory structures.

Case 3: Testis on right with a vas. No record of uterus and oviduct. On the left an ovary with uterus and normal oviduct, no male accessories. This might have been a "gynandromorph."

Case 4: Ovotestis on each side, male and female accessories on each side, but the oviduct on each side was blind. This case was seen by the writer.

It may be noted that the statement in "Sex and Internal Secretions" (page 215) that for cattle "hermaphroditismus verus is unknown in the literature" is incorrect.

*Bos indicus*. One case. Ovary on right with a vesti-

gial vas deferens and no epididymis; uterus and oviduct normal. Testis on the left with vas deferens and epididymis; a short blind uterine horn with no oviduct.

*Capra hircus.* We have found six cases including one unpublished case observed by Asdell (Cambridge, no. 35). Of these four were with ovotestes on each side, one with testis on the right and ovotestis on the left, and one testis on the left and ovotestis on the right. The descriptions of the accessory organs are very incomplete, but in three the uterus and oviducts are described as infantile (two with oviducts closed at the abdominal end). An epididymis is associated with the two testes and in one goat it is mentioned as associated with an ovotestis. The case, Cambridge 35, was a mature goat with ovotestes on each side. The epididymides and vasa deferentia were fairly well developed on each side. The uterus was bicornuate but the oviducts were short and blind at the ovarian end.

*Sus scrofa.* The pig has produced by far the greatest number of recorded true hermaphrodites. We have found fifty-one cases and doubtless there are others. The distribution of the gonads in forty-eight of these cases may be interesting.

<i>Right Side</i>	<i>Left Side</i>	<i>Cases</i>
Testis	Ovary	14
Ovary	Testis	3
Ovotestis	Testis	7
Testis	Ovotestis	2
Ovotestis	Ovary	6
Ovary	Ovotestis	1
Ovotestis	Ovotestis	15

“Sex and Internal Secretions” (pp. 208–9) gives the case described by Corner (1920) as the only one with testis on the left and ovary on the right. Dr. Corner in a personal communication remarks that this statement is due to a mistake in the original description. His pig had a testis on the right side and an ovary on the left. It was described correctly elsewhere (Corner, 1921). There

are, however, other cases in the literature to which the description would apply, but the reversal of the image in photographic reproduction has been known to create confusion.

A review of the literature on the pig shows that the uterus is always present on both sides, on the side with the testis as well as on that with the ovary. The oviduct is usually absent or vestigial on the side of a testis, and generally vestigial or sometimes absent on the side of an ovotestis. Male accessory structures are absent or occasionally vestigial on the side of an ovary, but normal on the side of an ovotestis. It would appear that the presence of testicular tissue does not suppress the development of the uterus and oviduct completely, but it does suppress it to some extent on the testis side. Male accessories do not suffer in the presence of ovarian tissue provided that testicular tissue is associated with it. In the absence, however, of testicular tissue, the male accessories are impaired even to the point of suppression. In general, also, the cases in other mammals with bicornuate uteri conform. Notable exceptions are the guinea pig and cat. The latter conforms only partially.

Amongst the pigs certain exceptions occur. These are: Krediet (1933) C6, normal oviduct on testicular side and no male accessories on the ovarian side; Davis and Pack (1927), oviduct normal on the testicular side; Møller-Sørensen (1916-7) I, epididymis and vas deferens on the ovarian side, and IV, epididymis with no vas deferens on the testicular side.

It should be mentioned that many reports of hermaphroditism leave much to be desired in the matter of compilation and description. Møller-Sørensen's report, however, is a model of clarity. Although there is considerable room for error in analyzing the data available, yet the general inferences are so strongly supported that we put them forward without hesitation. We can not draw a distinction between species with a duplex uterus and those with a bicornuate uterus; the difference in

behavior appears to be between rodents and ungulates. The ground squirrels conform to the ungulate pattern, but the guinea pig does not. Evidence from other orders is too scanty to make a generalization.

Baker (1925-6) has noticed some of the differences which we describe in this paper, but the data which he considered were too limited to allow him to generalize. His summary of the problem is as follows: "Some influence other than the gonad hormones affects the development of the accessory reproductive organs. This influence is swamped by either gonad hormone acting alone, but shows itself when both testicular and ovarian hormones are present to counterbalance one another." This does not appear to be a very good analysis, since it fails to take into account the peculiarities observed when the gonads are not the same on both sides. There is a positional effect upon which the hormonic effect is superimposed.

The pig reported upon by Følger (1932) is interesting, as this intersexual pig was pregnant. On the right side was a uterus with an oviduct and infundibulum and an ovary containing fifteen corpora lutea. On the left side the uterus tapered to a point. A testis with an epididymis and vas deferens was present on this side. There were four foetuses in each horn. Spermatogenesis was not occurring.

#### E. PRIMATES

*Homo sapiens.* We have not reviewed the literature on hermaphroditism in man in detail, as that has been done carefully by Young (1937). We have contented ourselves with an examination of the cases he cites. Several of these are useless for our purpose, since the accessory sex organs are not reported upon in detail. In general, the details given support the inferences drawn from other species, but there is little or no mention of the patency of the fallopian tubes. The main difficulty in gathering data is that most of the information is obtained at operation. Very few of these cases come to autopsy.

There is evidently a strong tendency toward the conversion of the simplex uterus into a bicornuate uterus. The form of the uterus is occasionally given: bicornuate (autopsy); small, normal shape (not autopsy); cornuate (not autopsy); bicornuate, two cervices (not autopsy); bicornuate (autopsy); bicornuate (autopsy); rudimentary (autopsy); normal (not autopsy); unicornis (not autopsy); malformed, ill-defined cornua (autopsy). All the autopsy specimens record an abnormality of the uterus.

One may speculate that this represents a reversion to a more primitive state.

#### SUMMARY

1. The difficulties in the current views of the embryonic and hormonic development of the accessory sex organs in true hermaphroditism are discussed.
2. The view is advanced that development of the accessory reproductive organs is influenced by the nature of the gonadic tissue on the same side. We believe that a positional effect is exerted which modifies the ability of the hormones to express themselves. This seems to be due to structural modification.
3. Gynandromorphism or hermaphroditismus verus lateralis with corresponding accessory sex organs has appeared only in rodents.
4. In ungulates the uterus develops on both sides, regardless of the nature of the gonad. There is one possible exception. But the oviduct is usually vestigial or sometimes absent on the side of an ovotestis or testis. Male accessory structures are absent or occasionally vestigial on the side of an ovary, but normal on the side of an ovotestis. Male accessories do not suffer in the presence of ovarian tissue, provided that testicular tissue is associated with it. They do require the presence of testicular tissue for their adequate expression. Female accessories, on the other hand, develop in the absence of ovarian tissue, but their full development in the region

of testicular tissue is hampered. These findings apply also in part to rodents.

5. In primates (man) there is a strong tendency for true hermaphroditism to be associated with a bicornuate uterus.

#### LITERATURE CITED\*

- Baker, J. R.  
1925-6. *Jour. Anat.*, 60: 374-381.
- Corner, G. W.  
1920. *Contrib. to Embryology*, 54: 137-142.  
1921. *Jour. Urol.*, 5: 481-489.
- Davis, A. H., and G. T. Pack  
1927. *Endocrinology*, 11: 313-320.
- Følger, A. F.  
1932. *Acta path. et microbiol. Scan., Suppl.*, 11:143-150.
- Krediet, G.  
1931. *Zeit. f. anat. u. entwicklungsgegs.*, 94: 39-53.  
1933. *Acta veterinaria neerlandica*, 1: 7-120.
- Lillie, F. R.  
1931. *Science*, 74: 387-390.
- Møller-Sørensen, A.  
1916-7. *Maan. f. Dyrl.*, 28: 433-444.
- Wiesner, B. P.  
1934. *J. Obst. and Gyn. British Empire*, 41: 867-922.  
1935. *J. Obst. and Gyn. British Empire*, 42: 8-78.
- Young, H. H.  
1937. "Genital Abnormalities, Hermaphroditism and Related Adrenal Diseases." Williams and Wilkins Company, Baltimore.

\* This bibliography is a list of papers cited during the course of the argument in this paper. It is not a bibliography of all the papers consulted to obtain the characteristics of each case considered. A fairly comprehensive bibliography has been compiled. This has been mimeographed and will be sent to any one who wishes a copy. It may be obtained from Dr. S. A. Asdell, Laboratory of Animal Nutrition, Cornell University, Ithaca, N. Y.

## TOLERANCE IN ANTS

DR. LAURENCE J. LAFLEUR

NEW YORK, N. Y.

ACCORDING to popular opinion, the ant is a highly beligerent being who has only to meet another insect—even an ant of the same species but of another nest—to grapple with it in mortal combat. This is probably true of some few species out of the thousands known, but in general the very reverse is the case. Except when slave-making ants make raids on their neighbors, and when spring competition for extra land causes wars, the ants of the northern states are a peaceful lot. When two ants of different nests meet, the behavior most frequently witnessed is the recoil of both ants, and their subsequent pursuit of their peaceful occupations.

Even when one party is so large or so numerous that it risks nothing in attacking and killing the alien, there is usually a perceptible hesitation about proceeding to extreme measures. Miss Field<sup>1</sup> writes:

An instance of this toleration was given by a queen and one worker major that had been isolated in a Petri cell for more than three months. After killing several older callows, introduced one by one, they had permitted an alien minim, introduced when but a few hours old, to remain with them. Five days later I introduced two sisters of their adopted young worker, the newcomers being minims about twenty days old. These newcomers at once attacked the queen and the major. The major acted solely on the defensive. Curling her abdomen in, and sitting on the small of her back, with her tough thorax presented to her small enemy, she permitted much nabbing of her body and much pulling of her limbs, making no retaliation. The queen, on her part, caught her little adversary by its antenna and held it firmly and quietly for some minutes, then released it and stood head to head with it without nipping it. The whole conduct of the adults was like that often seen in big dogs that are playing with obstreperous puppies. It appeared as if the adults liked their adopted callow and were unwilling to harm its sisters. The three callows perfectly affiliated from the start; but the newcomers often renewed their attacks on the queen and the major, and after some hours were killed by the adults. The adopted callow continued to live in that cell.

On many occasions, this tolerance is reciprocated, re-

<sup>1</sup> *Proceedings of the Academy of Natural Sciences*, pp. 427-428, 1901.

sulting in the formation of mixed nests. In fact, it is the rule rather than the exception that mixed nests can be freely formed of not too dissimilar species, provided that only small numbers of ants are present. Even in Miss Fielde's experiment, the result would probably have been favorable if each of the callows had been introduced separately and thus allowed to become acquainted with the queen and major in the absence of its own sisters. I have used this method with much success in the formation of mixed nests.

Forel,<sup>2</sup> who experimented extensively on these lines, writes:

I have seen a starving female *Formica pratensis* placed in a bowl with some working ants, *pratensis* and *sanguinea*, though repelled at first by individuals of its own species, then beg for disgorged food from a *sanguinea* belonging to a strange swarm, and receive it. The friendly act of the one called out reciprocity, in spite of the "hostile odor." From that moment the female *pratensis* joined the *sanguinea* definitely against the *pratensis*. I have observed several cases like this, and they afford much food for reflection.

An emotional rather than a mechanical reaction to the unusual situations provided in these experiments is commonly suggested, as in the cases already cited. Another clear case, which throws some incidental light on methods of communication and differences of individual intelligence, was observed by the present author.

A few workers of *Lasius niger* were given larvae and pupae of a number of different species. They accepted unhesitatingly the young of *Lasius flavus* and *mixtus*, *Formica rufa*, *Pheidole* (a Myrmecine ant) and even *Ponera pennsylvanica* (a very primitive form). After some hesitation they accepted the young of the tiny semi-parasitic ant *Solenopsis*, but they altogether refused the much more closely related *Prenolepsis*. I added a few workers from other nests, which were readily accepted, until the colony consisted of ten *L. niger* workers from five different nests, and a huge pile of assorted larvae and pupae. I then added ten workers from a sixth nest.

<sup>2</sup> *International Monthly*, Vol. 5, pp. 722-723.

There was a small amount of fighting, which soon ceased, no damage having been done, and the twenty niger workers consorted peacefully.

I then added a small *L. mixtus* worker that had been isolated for a day or two. She sought the larvae, being more concerned with them than the niger workers, and was friendly towards the occupants of the formicary. But the attitude of the others was dubious. Time after time one or more niger workers would bite her legs and pull. Usually the mixtus was able to cross antennae with the niger, which resulted in the latter's letting her go in less than half a minute. Even when four to six were holding her, if she crossed antennae with any one, that one would let go and thus enable her to conciliate more of her captors. But occasionally she would be so held that no antennal communication was possible, and then she remained until I disturbed her captors sufficiently to allow her to stroke the antennae of one of the niger. The first time this happened, I waited fifteen minutes before I intervened, on the second and third occasions I interfered almost immediately. The *Lasius niger* seemed no nearer amity with the mixtus after a day of this sort of behavior than at the beginning, and I had long since become impatient of their failure to learn; but it was only after being released by my intervention for the third time that the mixtus seemed to lose patience. She retired to the far corner of the formicary, and when one of the niger wandered near, attacked her unexpectedly and, despite her larger size, killed her handily. A second was similarly despatched, and as the mixtus seemed quite competent to annihilate my little colony, I removed her and took her back to her own nest.

The individual emotion suggested in these observations is confirmed by other reports. Forel<sup>3</sup> has described cases of "cold-blooded fighting" that "might well be called torturing." There are many more cases of

<sup>3</sup> *International Monthly*, Vol. 5, p. 572.

benevolence, some of which I have collected in "Helpfulness in Ants."<sup>4</sup>

One other case of individual emotion I can not refrain from quoting here. In reading it, it is well to remember that males, under natural conditions, mate with the females for a few minutes during flight, and die at the end of the day. Miss Field<sup>5</sup> writes:

The history of this little pair illustrates interesting traits of these ants. The two were taken from different colonies on a sunny morning after heavy rain, September 17, 1900. They were immediately placed by themselves in a Petri cell, and were at once friendly. The courtship or honeymoon was distinguished by mutual devotion. The one was rarely beyond the touch of the other, and the satisfaction of the two in their companionship was apparently equal. If the queen moved the king usually followed. If the king failed in constancy of attention to her, the queen approached and by a side stroke of her antenna made him aware of herself. The queen was exceptional in retaining all her wings until after she deposited her first two eggs, on the 15th of November, two months after swarming. She had laid twenty-eight eggs before she lost the wings of one side, on December 7, and she laid many more before her last wing fell off in January.

From the first egg-laying, the king and queen both watched over the eggs, one of them remaining on guard when the other went to the opposite side of the cell to eat. The king watched over the eggs in the absence of the queen, but he never lifted them nor carried them about as did the queen.

On the death of the king, December 28, after more than a hundred days of wedlock, as he lay prone on his back with outspread wings, the queen piled her twenty eggs upon him, and hung over the body persistently. On the ensuing days I separated the body, the queen and the eggs, first by a distance of a half-inch, then of an inch, then of two inches, then of three inches, and in a few hours after each separation the queen had brought the body and the eggs together again and stood with her head lowered over them, her mouth usually near the king's mouth. On the fifth day after his death, I moved his body to the opposite side of the cell, and separated it from the eggs by an intricate route between the sponges. The distracted queen at once set out in search of her treasures, and in her efforts during the next two days to bring the body and the eggs together, she so scattered the eggs that, fearing the loss of them, I took out the shriveled body, collected the eggs, and left the queen alone with them in a cleaned cell.

Two males, one the issue of a worker's egg, the other of a queen's egg, were later on introduced separately into her cell, and were killed and dismembered by her.

Preference for peace rather than war may be shown by whole communities, and there are several cases re-

<sup>4</sup> *Jour. Comp. Psychol.*, August, 1940.

<sup>5</sup> *Proceedings of the Academy of Natural Sciences*, pp. 442-443, 1901.

corded where two communities thrown together have joined forces, either without or after fighting. One of the more interesting observations is by Forel.<sup>6</sup>

*Formica sanguinea* and *Formica pratensis* are two species inveterately hostile to each other and always at war. I chose two populous swarms and put into the same bag a large number of ants of each of these species, mixing and jumbling the whole lot at once. During the course of the next hour great tumult reigned within the bag. At the end of that time I connected the mouth of the bag with an artificial glazed nest by means of a tube. The ants rushed into it in utter confusion, and greatly excited. Many were fighting; many were dead; every time individuals of the two species met, they threatened each other with their mandibles, and they were all a prey to terror. The sanguineae were first to recover their composure, and started to move from the bag to the glazed nest. The pratenses, though more suspicious, followed; the fighting soon became less fierce; the ants wounded in the first encounters died, and by evening there was only some squabbling and threatening. The next day, save for some instances of bickering, nearly all the ants were at work together. I then placed them in a larger nest, and in the course of a couple of days the alliance between them was almost perfect. On the fifth day of the experiment some minor quarrels broke out, but the sanguineae and the pratenses were beginning mutually to disgorge honey and to treat each other as comrades. Thereafter the harmony was complete. On the tenth day I let my ants loose in a meadow. They united in attacking a nest of *Formica rufibarbis* and settled in it, without exhibiting the least inclination to separate. The moving was done in common, the foes of a few days before helping and carrying each other. True, two or three sanguineae did exhibit some animosity and attacked some pratenses, but the latter let them have their own way and did not attempt to defend themselves. A small sanguinea hung on to the foot of a pratensis and died in the act. This was the end of the fighting, and the mixed swarm lived in perfect harmony within its nest. On the sixty-third day of the experiment, I took a handful of *Formica pratensis* from the original swarm, placed them within a few centimeters of my mixed swarm, and watched the result with the keenest interest.

This is what happened. The sanguineae attacked the newcomers quite fiercely, but without making use of their venom. The allied pratenses then came up and though they did not fight their former sisters, they started to remove their nymphae into the nest. The new arrivals showed themselves hostile to the sanguineae, and at the outset treated their former sisters rather badly, but they soon joined them, having no doubt recognized them, and allowed themselves to be borne to the nest by them. The sanguineae proved comparatively gentle in their treatment of those ants that were personally unknown to them, but the scent of which must have been the same as that of their new comrades. They plainly did not take them for the latter, however, and upset and bit them.

<sup>6</sup> *International Monthly*, Vol. 5, pp. 574-576.

A certain tolerance is commonly shown by slavemaking ants, who usually avoid killing as much as possible in their raids. Thus, when *Polyergus* is attacked it threatens its attackers with its pointed mandibles. This is usually sufficient: if not, one crunch kills the over-brave *Formica*. In describing a raid of *Polyergus breviceps* on *Formica subsericea* Wheeler<sup>7</sup> wrote:

From time to time a breviceps would emerge from the nest carrying a subsericea worker, take it a few centimeters from the opening and put it down. To my surprise the black ant scrambled to her feet and ran away uninjured. I saw this performance repeated more than a dozen times by different amazons. Not a single subsericea was killed or even maimed! The plundering of the nest continued, the breviceps returning repeatedly from their own nest to get more pupae. . . . On raising the stones I found a great many unharmed workers in the galleries but not a single larva or pupa. These ants must have remained in their nest during the whole time that the rape of their brood was in progress! The foray was remarkable on account of the behavior of both species, for the subsericea, though abundant, had made no attempt to protect the young which they had for weeks been rearing with infinite solicitude, and the breviceps had been more courteous and considerate than their vocation of professional kidnappers would seem to permit.

Mrs. Treat<sup>8</sup> gives another instance where ant armies, going through all the preliminaries of combat, yet stopped short of actual injury. She writes:

In the summer of 1881 I witnessed an exciting contest between two colonies of the same species, over a fine herd. The pasture on which the cows were feeding consisted of tender green herbage, and they were in good condition and yielded an abundance of the saccharine fluid. Around this pasture was a space of bare ground, where the troops were marshaled to keep the neighboring colony from trespassing among the drove. Tier upon tier, a solid phalanx extended around the entire pasture, making it impossible for the invaders to break through the ranks. The assaulting army was lean and hungry-looking, but fully as large and strong as the one attacked. There was no general engagement, but every little while two of the opposing forces would clinch and tumble about the ground like two dogs, but on relaxing their hold neither party seemed to be hurt. The cows were not neglected during this skirmishing. A host of kind and gentle milkers were constantly employed in obtaining the fluid, patting and stroking the cows with their antennae until they gave down the milk. I noticed that the soldiers often changed places, those at the front going to the rear. The cause was soon apparent. All along the rear the milkers were feeding the troops. Other milkers were constantly going to and from the subterranean city, which was

<sup>7</sup> "Ants," pp. 476-477, Columbia University Press, 1910.

<sup>8</sup> *Atlantic Monthly*, Vol. 54, pp. 331-332.

situated not far from the pasture-lands. They were no doubt supplying the queens and other members of the colony who were unable to be in the ranks.

After witnessing this skirmishing for several days, I established a drove of aphides near the city of the hostile colony. Some of the invaders were always on the road between the two colonies, slowly walking back and forth, like sentinels, to watch over their city, that it might not be taken by surprise while the protectors were absent. And now one of the sentinels came upon the cows, and ran around them in an evident state of excitement, but did not stop to obtain any milk. Apparently satisfied with the fine condition of the herd, she ran with all haste to impart the good news to the army stationed around the neighboring colony. I followed her closely, never losing sight of her amid the throng. On her way she frequently met a comrade, whom she stopped for a moment and touched with her antennae. The speed of the comrade after obtaining the news was greatly accelerated in the direction of home. The sentinel reached the outer ranks of the army, and communicated with everyone with whom she came into contact, and somehow imparted the same excitement with which her own body was quivering, until the whole army was aroused and on the homeward road. Very soon there was a host of eager milkers among the drove. But a large part of the army retired within the city, where they were fed by the milkers. Now that the invading force was withdrawn, the troops of the threatened colony also disappeared, only a few sentinels remaining to watch over the milkers and herd.

Sometimes formicine tolerance has the flavor of humor. McCook<sup>9</sup> writes:

A good example of the pugnacity and courage of ants is a small species (*Dorymyrmex flavus*), that digs its little nests upon the great open spaces surrounding the central mound of the occident ant of Colorado. A large commune of the latter which had been badly damaged by the wash of heavy rains was a scene of active rebuilding. Four moundlets of *Dorymyrmex* had been reared upon the pavement, one of them quite near a center of operations in one of the main tracks by which the workers had ingress and egress. Here an incessant warfare was being waged by the dwarfs upon their big neighbors. Every occident that essayed the passage to or from the ground was attacked. Squads of *Dorymyrmex* surrounded their single gate, and upon the approach of one of the occidents the nearest warrior flung herself upon the unconscious intruder. That she was alone, that there was such disparity in size between her and her adversary were facts that plainly had no part in her calculations.

It was curious to note the effect upon *Occidentalis*. She stopped instantly; drew her feet closer together; stiffened the legs, thus raising her body well above the earth; bowed her back; elevated her head; stretched out the sensitive antennae, as though to guard them especially from harm; and, in fact, presented an amusing likeness to the pose of a cat at the first onset of a dog. The fore leg upon which *Dorymyrmex* had seized, and which had instantly been raised, was then shaken violently, and the little assailant rolled upon the ground.

<sup>9</sup> "Ant Communities," pp. 195-198, *Harpers*, 1909.

Thereupon occident unbent herself and resumed her way. She had scarcely started ere her tormentor again was upon her, followed by another and another, until her body was dotted with the little vixens. They grasped her feet, fastened upon the under parts of the abdomen, mounted her back, seized her antennae. They could not be shaken off. She snapped at them with her strong jaws; struck at them with her claws; doubled her abdomen under her body, and thrust at them with her barbed sting. Some were crushed, some were thrown off, but others came to the assault. Anon the warring mass rolled upon the ground, a whirling mass of red and dark yellow, of quivering legs and antennae. At last the aggressors were driven off, or released their hold, and occident retired to a safe distance, combed her ruffed hair, and passed by on the other side.

Some of the occidents, as soon as they neared the *Dorymyrmex* bounds, paused, and stood quite still, as though reconnoitering the hostile quarters. The pause was fatal, for they were attacked at once by the vigilant sentinels, who sallied forth to a goodly distance upon the avenue. Others seemed to recognize that discretion is the better part of valor, and made a wide détour of the skirmish line of the little vixenish raiders. It was plain that the occidents thoroughly knew the qualities and temper of their involuntary guests, and regarded them with wholesome distrust, not to say fear.

The result of the guerilla warfare above described was rather remarkable. The next morning, upon visiting the ground, I found that the occidents had abandoned their old avenue, had cut down and around the *Dorymyrmex* colony, and made an opening on the edge of a slight ridge, several inches beyond the disputed territory, but still in the line of the avenue they had been using. A little of the pains required for this last would have cut out and carried away the whole *Dorymyrmex* nest space, whose contingent of diminutive warriors could have been overwhelmed in a moment by the legions of their huge hosts. Subsequently the occidents made an amusing retaliation upon their wee tormenters, for I found their nest literally buried under the dirt excavated from the new gangway, and dumped upon their gate and moundlet. It was a fitting and laughable punishment for the little churls, who, however, would probably cut their way out, unless the process were continued.

The latter process is apparently not infrequently resorted to by the agricultural ants. Lincecum<sup>10</sup> wrote:

They do not interrupt, in any way that I have discovered, the small black erratic ant, when it comes on their pavement. They even permit the erratic ants to erect cities on any portion of the incorporated limits, and do not molest them. It may be that the little fellows serve them some purpose. But when they build too many of their confederate cities on the pavement of the agricultural ant, it seems to be an inconvenience to them in some way, but they do not go to war with them, nor attempt to rid themselves of the inconvenience by any forcible means. They, however, do get clear of them, and that by instituting a regular system of deceptive and vexatious obstructions. The deception is manifest in the fact that it appears to have suddenly become necessary to raise the mound two or three inches higher, and also

<sup>10</sup> *Proceedings of the Academy of Natural Sciences*, p. 329, 1866.

to widen the base considerably. Forthwith are seen swarming out upon the pavement hosts of ants, who go rapidly to work, and bringing the little black balls which are thrown up by the earthworms in great quantities everywhere in the prairie soil, they heap them up, first at the base of the mound, widening till all the near erratic ant cities are covered up. At the same time, they raise the entire pavement an inch or so, and in prosecuting this part of the national work deposit abundantly more balls upon and around the erratic ant cities than anywhere else. The little ants bore upwards through the hard sun-dried balls, which are constantly accumulating—getting worse every hour—until the obstruction has become so great that they can no longer keep their cities open; and, finding that there is no remedy for the growing difficulty, they peaceably evacuate the premises. There is found on almost every pavement, at this season of the year, three or four small pyramidal mounds, that have been constructed for the purpose of crowding out the little erratic ants.

The size of the ants involved is typical. More often than not, it is the smaller ant who attacks tenaciously, the larger one who turns the other cheek and attempts to restore the peace. Miss Field has already compared this behavior to that of dogs: comparison with human behavior is perhaps more significant. Among men, the pacific nature of the powerful and intelligent arises from their sense of security, while the truculence of the physical, mental or economic underdog is the product of an inferiority complex. There is every appearance that this is true of dogs and ants as well as of men, and I see no reason to disbelieve these appearances. As McCook once said in another connection, the emotions of ants are often clear to the human observer. Despite the greater disparity between man and ant, there is no reason why we can not understand the behavior of the ant, in the same way, though not as completely, as we do that of the dog.

## EDITORIAL

WE print herewith a letter recently received from the Secretary of the American Society of Naturalists. It is with great pleasure that in this letter we are able to announce the list of advisory editors to THE AMERICAN NATURALIST appointed by the Society:

DEPARTMENT OF ZOOLOGY  
INDIANA UNIVERSITY  
BLOOMINGTON, INDIANA

*Mr. Jaques Cattell, Editor  
The American Naturalist  
Lancaster, Pennsylvania*

October 31, 1941

MY DEAR MR. CATTELL:

The membership of the American Society of Naturalists should know that at the annual meeting of the Society held in Philadelphia on January 1, 1941, the Society commended THE AMERICAN NATURALIST and urged that our membership give it all possible support. The Society expressed its appreciation of the long and valuable service which THE AMERICAN NATURALIST has rendered biology, particularly in the field of organic evolution, and recommended to our membership the desirability of giving THE AMERICAN NATURALIST individual support wherever possible.

In accordance with action taken at that same meeting, a committee of the Society has drawn up a plan for the organization of a board of consulting editors, and our Executive Committee has asked the following persons to serve in that capacity:

- Dr. W. C. Allee, University of Chicago
- Dr. C. W. Metz, University of Pennsylvania
- Dr. G. W. Beadle, Stanford University
- Dr. Th. Dobzhansky, Columbia University
- Dr. Karl Sax, Harvard University
- Dr. L. J. Stadler, University of Missouri
- Dr. A. Franklin Shull, University of Michigan
- Dr. L. J. Cole, University of Wisconsin
- Dr. C. L. Hubbs, University of Michigan

The Society feels honored in thus becoming definitely associated with a journal of such high standing as THE AMERICAN NATURALIST. We are also proud of the Editorial Board which

has consented to contribute its services to the further expansion of the journal and the work of the Society.

ALFRED C. KINSEY, *Secretary,  
American Society of Naturalists*

It is a great tribute to THE AMERICAN NATURALIST that those outstanding in the field of biology, especially in genetics and evolution, should accept this responsibility and give their time and thought to the continued excellence of the journal.

The subscription list is larger than it has been in many years in spite of the loss of foreign subscriptions, and it is hoped that those interested will subscribe when possible and encourage its acquisition by libraries.

There has been an increase of sixteen pages for each issue during this year. It is hoped that this increase may be retained and even enlarged by the demand for the journal both by subscription and editorial contribution.

Prompt publication of accepted manuscripts has become an increasingly difficult problem and the solution is more subscriptions and more pages.

JAQUES CATTELL,  
*Editor*

## REVIEWS AND COMMENTS

EDITED BY CARL L. HUBBS

IN this section reviews and notices are given of current publications on general biology and of specialized works which have an important bearing in the general field. Emphasis is given to books and major articles which fall within the special scope of *THE AMERICAN NATURALIST*, in that they deal with the factors of organic evolution.

REVIEWS AND COMMENTS are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as otherwise indicated, all items are prepared by the Section Editor, Dr. Carl L. Hubbs, University of Michigan, Ann Arbor, Michigan. All opinions are those of the reviewer.

**The Course of Evolution.** By Differentiation or Divergent Mutation Rather than by Selection. By J. C. WILLIS. Cambridge: University Press (New York: Macmillan Co.), 1941: i-viii, 1-207, figs. 1-10. \$3.00.

ANTI-DARWINIAN in the sense that it abandons natural selection as a prime factor in evolution, this book brings a considerable body of observation and some statistical data to bear on evolutionary problems. It is a sequel to the author's well-known treatise on "Age and Area."

Willis prefaces his new book with an explanation of how, in 1905, he came to a study of geographical distribution. He soon encountered a seemingly hopeless confusion in regard to the variation in the size of the ranges of species and groups, and in the number of kinds of plants in each group. This confusion, he says, is not the way of nature, whose "work is always beautifully planned, as Darwin had already shown in the wonderful theory of evolution." An early faith in natural selection was shattered by these systematic and geographical studies. The author's alternative explanation of "Age and Area" (1922) developed from his discovery, in 1912, of the "hollow curve" (which is obtained when one plots the frequencies of the numbers or the distributional areas of the species within a group). General criticism was accorded his theme that the age of a species or group suffices to explain its degree of differentiation and its area of occurrence, and that natural selection is consequently disproved. Despite this criticism "the writer's faith re-

mained unchanged, and he continued to follow up his beliefs" in inquiries which have resulted in "The Course of Evolution" and in a promised volume on the geographical distribution of plants.

It is admitted only that natural selection is of some significance in the survival and elimination of individuals and of local varieties—but not of species. The historical importance of the Darwinian factor is emphatically stressed (as a giant to be struck down?).

Convinced of the failure of natural selection to explain the facts of evolution, distribution, ecology and economic botany, Willis has turned to a compelling internal force, which, "working upon some definite law that we do not yet comprehend," forces a whole population to vary in the same direction. Rather unwise he names this force "differentiation," and regards it as "a kind of compromise" between special creation and natural selection.

As though to strengthen his alternative explanation of evolution (but more likely because of his early training), Willis grossly distorts the theory of natural selection as it is currently conceived. He keeps insisting, wrongly, that this theory has ignored functional characters. Emphasizing the criticisms of Jenkins (1867) and Maclaren (1877), but largely ignoring the facts and interpretations of modern evolutionary biology, he holds that no adaptive changes in individuals can ever be perpetuated in the race, because all would be swamped by crossing (unless the changes arose mysteriously in all plants over a considerable area). Without warrant the theory is limited to the supposed accumulation of infinitesimally small differences. In Willis's view the selection theory assumes that a new advantageous character becomes more and more marked in *each* generation, and that a new and better adapted form *must* displace its parent form (after having reduced it to one or more small-ranging relicts). With only partial justice natural selection is described as a cult. Willis feels that the Darwinian explanation of evolution breaks down because of these many assump-

tions; but he himself has advanced or retained them. Furthermore, he dislikes the selection doctrine as one of nature "red in tooth and claw," and as one which has been incorporated in certain political theories.

The author's evolutionary concepts, all of which he regards as contradicting the theory of natural selection, and as confirming his rival hypothesis of "differentiation," comprise the following ideas:

*Evolution proceeds by saltations.* The questionable evidence advanced to prove this concept need not be considered here, for large-scale mutations are not incompatible with the modern theories of selection, and hardly any biologist now looks on mutations as necessarily, or mostly, large. The argument that major groups have neither fossil or living connections certainly holds poorly for animals, since many "missing links" and common ancestors have been discovered.

*Extinction is a rare phenomenon.* The falsity of this assumption becomes at once apparent in the legitimate comparison of the increase of individual populations and of species populations. Both increases, since they are geometric, would, on the geological time scale, very soon overcrowd the earth—unless extinction were the general rule.

*The age of a species or group is proportionate to the area it occupies* (the age and area hypothesis). With little extinction, how long (geologically) would it require for each group to occupy all the earth, if barriers were ineffective? If barriers to dispersal are operative, as they no doubt are, their varying geographic pattern would certainly modify the rate of spread so enormously as to defy any simple comparison of the rate. Spacial factors would then be more significant than temporal ones (age) in determining the size of ranges (areas). The suggestion that related forms will react similarly to the environment, and hence will spread at about the same rate, is quite at variance with the differential habitat responses that very commonly characterize closely related forms. Just how the age and area hypothesis negates the principle of natural selection is not clear; the degree to which the theory is true and precise would simply call for an approximately similar amount of selection on the related evolutionary lines.

*Supporting the age and area hypothesis are the hollow curves which result from the plotting of the frequencies of the number of*

*species, or of size of species ranges, within a genus or larger group; this relation brings evolution "into line with other sciences which have a mathematical basis."*" In the July, 1941, number of *Ecology*, Sewall Wright, our leading mathematical student of evolution, adequately proves that the "hollow curve" data do not demand the evolutionary interpretations of Willis, and further shows how Willis has neglected the findings and interpretations of the modern population theory of evolution.

*Primitive species or groups occupy small areas and highly-evolved ones are wide-ranging.* On the contrary, it should seem completely obvious to-day that the stage of evolution has no necessary correlation with the size of the range. That old relict plants and animals typically have restricted ranges is commonplace knowledge (and is partially admitted by Willis). Most biogeographers would agree that local endemics may be either autochthonous or relict. Perhaps most kinds of organisms occupying small areas are recent productions, but an indeterminate number can be assumed to be very ancient types, as well as representatives of all intermediate age classes.

*Degree of differentiation and the number of diagnostic characters increases "downward" (toward smaller categories) in the phyletic scale; evolution proceeds downward from family to subspecies.* In the reviewer's judgment this condition would result from the greater opportunity, in the larger groups for parallel adaptations to the limited number of ecological niches. Willis's interpretation, in so far as family origins are concerned, has some plausibility, for the single or few prime characteristics of some major groups often appear to represent the rare evolutionary discoveries that have opened the way for new outbursts of radiative adaptation. However, the first transition from the old group to the new would involve only an ordinary speciations process. The new group (that is, the new cluster of genera), would not have been formed until the new radiative adaptation was well under way. It becomes therefore a matter of words, or an arbitrary point of view, to speak of evolution as proceeding downward from family to subspecies rather than upward from subspecies to family. Willis's figure of downward evolution in a group of genera becomes a fairly conventional family tree if we turn his page upside down. Whether the production of the original family ancestor (basic genus A) was consummated in

one leap or by more gradual speciation is a separate problem, which hardly permits of a categorical or simple solution.

*Rate of evolution as well as rate of dispersal is similar in related groups.* This necessary basis for the age and area hypothesis is palpably absurd, for evolutionary rate varies widely with both genetic potential and the biotic pressure. Evolution in newly available areas has been so rapid as to justify the attributive, explosive. Paleontology also refutes this phase of Willis's hypothesis.

*Endemic species of the insular type usually belong to speciose genera.* Naturally.

*On any one island or other restricted area the endemic species tend to have small ranges; those which range widely over the world have wide ranges in the local area.* To a considerable degree the area occupied locally by the species may have been determined by its local age (period of residence), but surely factors other than this one stressed by Willis often enter in. The restricted distribution of endemics may of course be due to their youth, but may also be due to adaptations to a highly specialized habitat, to some reduced capacity for dispersal (like winglessness of insular insects, in itself an adaptation), to an inability to survive except under special conditions in the physical or biotic environment. Wide-rangers as a whole presumably have generalized habitat responses, which would give them a wide range too in the local area, but this feature may be one of phyletic youth as often as it is one of old age. It seems utterly bold, to the point of foolishness, to attempt a precise evaluation of the differential significance of such factors.

*Evolution proceeds without adaptation; the characters of systematic groups are nonadaptive.* Some accept this view for larger groups, some for the smallest groups, few for both. Others, including the reviewer, interpret most characters as being primarily or secondarily adaptive, in terms of their combinations and of the usual habitat of a given kind or group. The differential, compensative, and parallel aspects of adaptation that seem to dominate the evolutionary picture are scarcely seen by Willis. Nor does he adequately appreciate the force of the clear evidence, presented by modern mathematical geneticists, that very slight average sectional values can lead to speciation.

*Within a species local adaptations, as to climatic conditions, may occur, but this is not significant in evolution.* It is allowed by Willis that local adaptations, as to climatic conditions, may

occur within a species, but he does not admit that entirely similar adaptations may also characterize species and genera. Here we again find reared a distinction between microevolution and macroevolution (see review of Goldschmidt's views in these columns for May-June, 1941).

Willis points out wisely that "though Darwin's immortal service was really the establishment of evolution, the name Darwinism became attached rather to the theory of natural selection." It is this theory that Willis objects to, and attempts to supplant by an alternative explanation. He feels that "evolution itself is now so well established that it has no longer any need for any assistance or support from the hypothesis of natural selection." Many students, however, would regard the whole structure of evolutionary theory as a very shaky one, were the props of natural selection removed as completely as Willis has tried to knock them out.

**Studies on the Physiology, Genetics, and Evolution of some Cladocera.** By A. M. BANTA. Washington: Carnegie Institution of Washington, Paper No. 39, Department of Genetics, 1939: i-x, 1-285, diag. 1-16, figs. 1-170. \$2.50 (paper), \$3.00 (cloth).

To those interested in fundamental problems of biology, and especially to those desirous of studying aquatic organisms which are easy to culture and possess a variety of possibilities for experimentation, "Studies on the Physiology, Genetics, and Evolution of Some Cladocera" will be a welcome contribution to the literature. The possibilities for study of mutations and different phenotypic expressions of identical genotypes in these diploid parthenogenetic animals are indicated as especially intriguing.

After accounts of selection experiments, sex intergrades, mutations, control of "Male and Sexual Egg Production," "Genetical Studies in Sexual Reproduction," growth studies and the section on the effects of environmental conditions on phenotypes of *Daphnia* characters, the last portion of the paper is devoted to "Adaptation and Evolution." The discussions of adaptive

characters and of advantages of parthenogenesis are provocative of interest and philosophizing. In dealing with the evolution of parthenogenesis in Cladocera more information concerning the marine Cladocera would have added much interest.

Lastly the challenge "to some careful, ambitious, and energetic young man with long-lived forebears" to clear up the "endless confusion in the classification of these animals" might well receive serious consideration by those possessing the qualifications indicated.

JACK S. DENDY

**The Salamanders of New York.** By SHERMAN C. BISHOP. N. Y. St. Mus. Bull., 324: 1-365, figs. 1-66. \$1.25.

EXPERIMENTAL embryologists and other biologists using the tailed amphibians as material in their investigations will join herpetologists in their gratitude to Dr. Bishop for this full compendium of published and original information on the natural history of the salamanders which occur in New York. Items stressed include systematic character of eggs, recently hatched larvae, older larvae and adults (separate keys are given for each stage); sexual dimorphism; migrations and breeding habits; general habits; food; habitat (typical sites are figured); general range; and distribution in New York (detailed and mapped). The illustrations of the several life-history stages are of particular excellence and value.

**Variation, Isolation Mechanisms, and Hybridization in Certain Toads.** By ALBERT P. BLAIR. *Genetics*, 26: 398-417, figs. 1-6. **Isolation Mechanisms in Tree Frogs.** By ALBERT P. BLAIR. *Proc. Nat. Acad. Sci.*, 27: 14-17, fig. 1.

THESE significant papers indicate that anuran species are capable of hybridization in nature as well as in the laboratory, and that toad hybrids appear to be rather readily produced and may be fertile. Differences in time and site of breeding and probably in responses to mating calls are indicated as providing an isolating mechanism of considerable though not complete efficacy. It is hoped

that the author will present in more detail the evidence on the occurrence of hybrids in nature and on the characters of the experimental hybrids and their presumed natural counterparts.

#### NOTICES OF NEW BOOKS

**Preface to Eugenics.** By FREDERICK OSBORN. New York: Harper and Bros., 1940: i-xi, 1-312, figs. 1-12. \$2.75.—Starting with an elementary discussion of human genetics this excellent introductory volume on eugenics gives, in well-organized form, the results of researches on social psychology, vital statistics, populations and environmental relations. It closes with chapters on "Eugenic Reorientation of Various Social Policies" and "The Significance of the Eugenics Philosophy."

**About Ourselves.** A Survey of Human Nature from a Zoological Viewpoint. By JAMES G. NEEDHAM. Lancaster, Pa.: Jaques Cattell Press, 1941: i-xi, 1-276, 44 figs. (by William D. Sargent). \$3.00.—Making no pretence at the sort of treatment that might be given by a corps of specialists, the veteran entomologist and limnologist of Cornell talks about man, first as an animal and then as a social creature. He proves himself to be a wise philosopher, with an enjoyably quizzical sense of humor. He has furthermore the rare gift of speaking his listeners' language. It would do the whole nation a world of good to read this book.

**Under the Sea-Wind.** A Naturalist's Picture of Ocean Life. By RACHEL L. CARSON. New York: Simon and Schuster, 1941: i-xix, 1-314, 8 pls., 27 figs. (by Howard Frech). \$3.00.—A wise selection by the Scientific Book of the Month Club, this series of essays on marine life combines an appealing literary charm with thorough scientific soundness. The gifted author is a member of the staff of the Fish and Wildlife Service. The Glossary will give the public a much wider knowledge of the sea and its life.

SHORTER ARTICLES AND DISCUSSION  
SURVIVAL VALUE OF VARIETAL CHARACTERS  
IN SNAKES<sup>1</sup>

It is a recognized and a serious defect of biological theory that natural selection (an elimination of certain variants by diverse processes in the usual course of events; differential survival) has remained so much a matter of logical deduction and so little a matter of observation and of experiment. Robson and Richards (1936) cite only nineteen attempts to show that differential elimination takes place. Most of these are concerned more with showing a particular cause (preferences of particular predators, etc.) for differential elimination than in demonstrating the existence of a general process. All of them are severely, even devastatingly criticized by Robson and Richards.

I am concerned here with doing two things. First: to show that in snakes there may be at times and at places and in certain species very drastic selective elimination by natural causes not at all known or even inquired into; that this elimination affects characters subject to individual variation, but which are used by herpetologists in the discrimination of varieties, races, species and genera; and that much if not all of the variation subject to such elimination is hereditary and hence the elimination affects descent with modification. Second: to point out to my colleagues in herpetology a method which may produce results which will affect not only herpetology but also general biological theory.

In 1935 I had occasion to examine a collection of *Conopsis nasus* from Alvarez, San Luis Potosi, Mexico. I found considerable variation in the scalation of the head, and was surprised to note that this (a matter of reduction) was largely confined to the smallest specimens. It struck me at the time that this might prove an interesting and powerful method for demonstrating a selectional process in nature, that there might be already in print data which could be examined to see if the variation of the young differed from the variation of individuals of reproductive size, and that it might be well if other herpetologists were apprised of the possible existence of such a phenomenon and advised to distinguish between young and adults in variational studies.

<sup>1</sup> Contributions from the Department of Biology, Haverford College, No. 55.

I discovered that three papers along this line were published over thirty years ago. Weldon (1901), working on the snail *Clausilia laminata*, found that the range of variability of the young exceeded that of the adults. The same author (1904) working on *Clausilia itala*, found no difference between the variability of young and adult specimens. Di Cesnola (1907), working on the snail *Helix arbustorum*, found that the range of variability of the young exceeded that of the adults.

These findings have been criticized by Robson and Richards (1936) on the grounds that the observed differences might be due to "greater plasticity of young as well as to selection"—whatever that may mean. The criticism, however, may indicate that snails are not suitable material for this sort of work.

The scalation of snakes is known not to be subject to environmental modification from birth on. The number of body vertebrae and tail vertebrae, which is reflected in the number of ventral and caudal scales, is possibly subject to prenatal environmental influence, since some correlations have been made between environments and counts which hold for many species, of which the most striking is that insular snakes have more caudals than their mainland relatives. Further investigation is needed, but constant differences in such counts, between related forms which exist in the same region, seem to indicate that the ventral and caudal count of snakes is hereditary and not subject to prenatal environmental influence.

Head scalation might also be subject to prenatal environmental influence. That this is not so is strongly indicated by the data in my first published paper (1915). In this I pointed out that a variation (double loreals) so rare that I am unaware of any other report of it, occurred in a female *Natrix fasciata sipedon* and in one third of her brood. The chances of this trait not being hereditary are negligible.

There have not been lacking hints that scale characters (or other characters closely connected with them) have some effect on viability.

Blanchard (1921, p. 202), dealing with the available specimens of *Lampropeltis triangulum triangulum* from the vicinity of the District of Colombia and the Coastal Plain to the east, which show "more or less reduction in scutellation and pattern" says "more than half of the specimens are very small, and perhaps some of the aberrant ones would have died a natural death if they

had not been found and preserved. It is a fact that some of the most aberrant individuals, [of *Lampropeltis* in general] described and not described, have been juveniles."

Klauber (1936, p. 197) says of rattlesnakes: "broods . . . often seem to contain freaks . . . which probably would not survive in nature." ". . . a defective juvenile female *lucasensis* with 170 ventrals; the lowest normal individual has 183."

Smith (1938, p. 115) says of a brood of *Farancia abacura abacura* from Ft. Lauderdale, Florida, that it contained "nine" with "variations not found in adults or other young."

A collection of 23 *Conopsis nasus* Günther, taken by Dr. Henry Pilsbry at Alvarez, San Luis Potosí, Mexico, in 1934, was studied by me in 1935. The variations in the head scales include: loss of the loreal; reduction of postoculars from 2 to 1; reduction of the upper labials (from the maximum and usual number of seven) to 6 or to 4.

Of the 23 specimens, eight, with head + body length of 85–117 mm, are considered juvenile. Fifteen, with head + body length of 160–260 mm, are considered adult. Eleven (73.3 per cent.) of the adults show no reduction; four (26.7 per cent.) show some reduction. Three (37.5 per cent.) of the young show no reduction; five (62.5 per cent.) show some reduction.

If each separate loss or fusion of a scale is counted as a separate variation, there are four cases of loss of loreal, on one side only, in the adults, and no reduction at all in postocular or supralabial count. There are, in the eight young specimens, ten labial reductions, three postocular reductions, and one loreal loss: a total of twelve aberrations. At this rate at least twenty-two aberrations in fifteen adults might be expected: actually there are four.

The fairly strong variational tendency towards reduction, evident in the young of this species in this locality, is scarcely noticeable in the adults. It would seem that a majority of the young with these variations do not become adults, and the minority of the young (with the opposite variations) form the majority of the adults.

Linsdale (1936, p. 233) reports without comment on a collection of 46 *Chilomeniscus stramineus* from Eureka, Baja California. Of twenty-three males, 17 had length from snout to vent 150–200 mm; 6 had 96–148.5 mm. The former lot showed a range of ventral counts of 107–114; the smaller specimens showed a range of 103–113, and 50 per cent. of them had less than 107. Of twenty-

three females, 16 had head-body length 160–215; seven a length of 84–157. The ventral count of the larger lot ranged from 112–122; that of the smaller was 107–116, and four (57 per cent.) were below 112.

In this snake, at this place, at least half of the young are of a variety which is not represented in the adult population.

Stuart (1941, p. 18, f. 1) points out that 30 per cent. of the smaller (below 400 mm total length) specimens of *Dryadophis boddarti boddarti*, at Medellin, Colombia, belong to a variety which is not represented in the population of larger individuals. Six of these young have 238–262 vertebrae (ventral and caudal counts combined); 14 small and 12 larger (400–1000 mm) have 265–293 vertebrae. Stuart draws the inference that the variety with fewer vertebrae does not live to reach maturity.

Dr. Joseph Bailey and myself examined the heads of 190 *Dryadophis melanolumus alternatus* from the lower Tuira valley in Darien, but found no notable differences in the variation of young and adult. The head scalation is very constant. In 337 heads of *Chironius carinatus* from the lower Tuira we also found constant head scalation and no notable difference between young and adult.

Scale differences of the sort mentioned above are, as is well known, not only matters of individual variation, but also are used in discriminating between races, species and genera of snakes. These characters are, therefore, not unimportant to the student of the evolution and phylogeny of snakes. Individual variation in these characters has long been known, and it is now obvious that variation may, in some way which I do not attempt to explain, affect the survival of the individual animal.

A demonstration that selective elimination of certain variants may occur in nature would, of course, be considerably enhanced by data as to how and why these variants are eliminated, but facts or speculations as to the method or the cause of the elimination are really irrelevant to any demonstration that a selective elimination takes place. Indeed, it is irrelevant to such a demonstration to prove that a character is hereditary. It is only necessary to show that the elimination is not an illusion caused by one variant turning into the other.

It may be that the obvious scale characters which distinguish the survivors from those eliminated are only outward and visible signs which accompany (by close linkage or as partial effects)

more serious and unseen differences. Long study of snakes in the field has convinced me that many of these scale characters are in themselves important to the life of the animal. There is a great deal of definite correlation between the type of scelation (whether of head or of body) with the habitat, with the type of food normally taken, and with the means employed to take and engulf that food. I regard many of the features of snake scelation as definitely adaptive; as adaptive as the fin arrangements of aquatic vertebrates or the dentition of mammals.

It would be of great interest to compare by this method two populations of the same form from two different environments or areas, and to compare two different races of the same species. Young and adults should not be compared unless the whole lot comes from the same place or from one topographic and climatic unit area.

Most of the published information on variation in snakes makes no mention of size of specimen. Authors have been demonstrating areal or spatial variation quite successfully, but have usually left out information that might have shown trends of variation and selection in one or another or all the areas concerned. It is to be hoped that this may be remedied in the future. It is possible that systematic workers might actually find that more distinguishable adult populations exist than are recognized at present, since the present practise of including all specimens in variational counts may tend to conceal real differences in the reproductive populations. The adult populations may differ, although the juvenile populations are indistinguishable.

EMMETT REID DUNN

#### LITERATURE CITED

- Blanchard, F. N.  
1921. *Bull. U. S. Nat. Mus.*, 114.
- di Cesnola, A. P.  
1907. *Biometrika*, 5: 387-399.
- Dunn, E. R.  
1915. *Proc. Biol. Soc. Washington*, 28: 61-68.
- Klauber, L. M.  
1936. *Trans. San Diego Soc. Nat. Hist.*, 8: 20, 185-267.
- Linsdale, J.  
1936. *Copeia*, 4: 232-234.
- Robson, G. C., and O. W. Richards  
1936. "The Variation of Animals in Nature." Pp. 1-425. Longmans, Green and Co.

Smith, H.

1938. *Copeia*, 3: 110-117.

Stuart, L. C.

1941. *Misc. Publ. Mus. Zool. Univ. Michigan*, 49.

Weldon, W. F. R.

1901. *Biometrika*, 1: 109-124.

1904. *Biometrika*, 3: 209-307.

THE ABNORMAL MEIOSIS OF *BENZOIN AESTIVALE*  
IN RELATION TO THE ORIGIN OF SEX  
CHROMOSOMES

ELSEWHERE the author has maintained that the so-called sex chromosomes in the Angiosperms are: (1) an evolutionary by-product among the chromosomes; (2) originating as a meiotic irregularity instigated by previous hybridization of the species; (3) perpetuated because the advent of the dioecious condition occurred simultaneously with periods of abnormal meiosis; (4) equally well explained without ascribing to them any important function in the determination of sex in an individual (Jensen, 1939, 1940).

To test further the validity of the above contention the author has studied microsporogenesis in *Benzoin aestivale* (L.) Nees, the common spice bush, which is generally unisexual, at least in this part of the country. Since there are but two generally recognized species of the genus *Benzoin* (*Lindera*) growing in eastern North America, there is a resemblance between the generic condition found in this instance and the genera represented by *Vallisneria spiralis* and *Helodea canadensis* for which sex chromosomes have been described (Winge, 1923; Santos, 1924). These plants are members of small genera in contrast to the usual situation wherein most plants having sex chromosomes belong to large genera in which hybridization is common and the advent of the dioecious condition is recent and as yet not fully stabilized. It was hoped that a study of *Benzoin aestivale* would shed some light on the origin of so-called sex chromosomes in small genera.

During microsporogenesis in *B. aestivale* the twelve haploid chromosomes are readily distinguished and display considerable difference in size and shape. One of the medium-sized chromosomes possesses a distinct behavior. Each half of the "pair" is shaped like a V having a constriction on each arm shortly above the base; a tripartite arrangement. During the heterotypic

metaphase the whole or the halves may lie at one end of the spindle, or the halves at opposite poles. Seldom does it follow the other chromosomes. Occasionally some of the remaining chromosomes divide prematurely or lag behind, but by the end of the anaphase only the odd chromosome will remain apart from the other chromosomes. In about 50 per cent. of the P.M.C.'s one or both halves are left outside the daughter nuclei. The odd chromosome persists through the homeotypic division and is often seen in the cytoplasm of the microspores, where it seems to degenerate. Consequent to this behavior, the largely perfect pollen is of at least two sorts, namely; one half containing the normal twelve chromosomes and the other half with only eleven. Nothing is known of the potency of either type. However, the slight structural imperfections did in nowise compare with the percentage of microspores which must be deficient in chromatin. More important, however, is the observation that the odd chromosome "pair" did not always seem to be composed of identical members. One unit often appeared to be larger than the other and at the time of disjunction a small bridge of chromatin was formed from which one unit apparently procured more material than the other. During the anaphase a difference in size was not always discernible. Undoubtedly there are those who would immediately conclude that this instance constitutes another case of X-Y sex chromosomes. The author does not think so. Even if a pair of heterochromosomes were present, other criteria must be satisfied. The significant point is the effort on the part of this odd chromosome to produce a heterochromosome effect, and it is quite conceivable that further differentiation and increased meiotic regularity will eventually establish a larger or smaller chromosome in the male plants of the species than will be found in the female complement. There seems to be good cause for regarding *B. aestivale* as being in a stage of sex chromosome evolution. The condition just described is quite similar to that found in *Ilex opaca* (Jensen, 1939) and *Smilax rotundifolia* (Jensen, 1937). The author has also studied an unusual process in a plant of *Silene latifolia* (*S. inflata* Sm.). Though generally hermaphroditic, gynodioecious individuals also occur. There seems to be a contemporary attempt on the part of some species of *Silene* to assume the unisexual habit and thereby produce a generic situation as found in the allied genus *Melandrium*; some

unisexual, some hermaphroditic, and some in various intermediate conditions. During microsporogenesis in the plant of *S. latifolia* under consideration, one of the twelve haploid chromosomes was commonly left out of the nuclei resulting from the heterotypic division. It frequently underwent the second meiotic division in the cytoplasm. Other meiotic irregularities are more pronounced in *S. latifolia* than in *Benzoin aestivale*, and clearly link the abnormal behavior of these odd chromosomes with disturbances caused by previous hybridization of the species.

A statement was made in the above paragraph to the effect that although a set of heterochromosomes may be present in the male of *B. aestivale* the author could not regard them as sex chromosomes. The conventional criteria would demand that the female lack a similar complementary pair, although conceivably the female might have a heterochromosome XX, and that the sex chromosomes be distinguished in the somatic cells as well, and that over a series of generations the same chromosomal difference occur in the males and the females. Were all these demands met, one still would not need to consider them to have any direct role in the determination of sex.

Let us examine a typical X-Y sex chromosome mechanism, such as that described for the now classical *Melandrium album*. The male plants carry the XY and are assumed to be heterozygous to sex. The females are supposed to be indifferent to the approach of the microspores of its own species, the resulting pollen tubes and the eventual male gametes—all the eggs are assumed to possess the same inert disposition toward the male factor; the females are homozygous to sex. Under such discriminating protection, the logical conclusion that the heterochromosomes are sex chromosomes is quite unavoidable. In view of the fact that it is the male which invades the female gamete, that the eggs of a unisexual species can hardly be equally disposed towards the sex of their progeny since every act of fertilization is really an act of intraspecific hybridization, and in view of the rapidly expanding knowledge of the physiological factors which modify or determine sexuality, another assumption would appear more in keeping with the facts. Why should not both sexes be heterozygous to sex? If the female plants of *Melandrium album* transmit to the megasporangia varying degrees of selective disposition, then the eggs which come from the surviving megasporangia will vary as to

disposition. Those eggs, or egg nuclei, which possess a stronger disposition towards femaleness would discover a more harmonious mate in such male gametes as possess a chromosome complement similar to that of its own. The union of such gametes would result in female individuals bearing the XX condition. On the other hand, those egg nuclei with weaker female tendencies would be less disposed to reject the sperm nuclei possessing the distinctly male type of chromosome or nuclear composition, the Y-bearing gametes. Plants from this type of union would be males. Since this interplay of two heterozygotes allows for considerable variability, the natural occurrence of intersexed individuals is to be expected, without resorting to the bizarre formulae deemed necessary under the conventional concept of sex chromosomes. Although the eventual distribution of the X and the Y chromosome from the male *appears* to determine the sex of the progeny, *actually* the sexuality may be determined by negative selection on the part of the female organ or its gametes so that the X and the Y are distributed in the females and males respectively because of sex determination. On the basis of the above reasoning, the author is convinced that the so-called sex chromosomes have no important role in sex determination but merely represent evolutionary by-products peculiar to races of Angiosperms which embark upon the unisexual habit at the same time that they undergo hybridization. The author feels confident that further investigation will disclose many additional forms, of which *Benzoin aestivale* is but one, which will exhibit all the stages in the origin and development of so-called sex chromosomes in keeping with the hypothesis here propounded.

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LITERATURE CITED

- Jensen, H. W.  
1937. *Cytologia Fujii Jub.* Vol., 96-103.  
1939. *La Cellule*, 48: 49-60.  
1940. *A. M. NAT.*, 74: 67-88.  
Santos, J. K.  
1924. *Bot. Gaz.*, 77: 353-376.  
Winge, Ø.  
1923. *C. R. Trav. Lab. Carlsberg*, 15: 1-26.

